# THE RELATIONSHIP BETWEEN SUCCESSION AND THE RECOVERY PROCESS IN ECOSYSTEMS

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## INTRODUCTION

Succession is one of the oldest, most basic, yet still in some ways, most confounded of ecological concepts. Since its formalization as the premier ecological theory by H. C. Cowles and F. E. Clements in the early 1900s, thousands of descriptions of, commentaries about and interpretations of succession have been published and extended inconclusive controversy has been generated. Withal, no effective synthesis of the divergent observations from many different ecosystems, terrestrial and aquatic, has produced a body of laws and theories which ecologists, generally, have embraced. Repeated symposia on succession and the corollary problems of the succession concept, the community (or the ecosystem) and climax (equilibrium or stability in any of its several meanings) have not produced notable convergence of thought. Problems of conceptualization and terminology are still evident after three quarters of a century. The "new ecology," or better new ecologies, arrived on the post-World War II scene providing different approaches to the basic problems of ecology and succession; but the much sought after synthesis seems as elusive as ever. Recent years have seen a flurry of papers which have brought the entire concept of succession into question, and some purport to provide new insight, improved terminology and clearer direction for succession. For a consensus, however, we may be reduced to the elementary statement of succession provided in the answer to the riddle of the Sphinx—all this too shall pass away.

The apparent intractability and continued contradictions of the succession question, after many decades of study, lead to the suspicion that there is more involved than a straightforward, matter-of-fact, scientific consideration. This suggests that ecology, and the succession concept are in the midst of a revolutionary change, a change in paradigm, which is described by Kuhn [1970] as the way in which a scientific discipline progresses. Certainly, the terms revolution and paradigm, which are the keys to Kuhn's ideas, have appeared frequently in recent ecological papers [MacFadyen 1975; Goodman 1975; McIntosh 1975; Johnson 1977; Simberloff 1978]. One way of clarifying recent discussions concerning succession, which will be considered in this chapter, is to look at the history and the organizational pattern of ecology. Burgess [1977], in a history of the Ecological Society of America, showed that after 30 years of no growth, membership increased exponentially since 1950. Parallel to the increase in the number of ecologists, there has been increased heterogeneity as ecologists were required to face important scientific and empirical problems. The response to the challenges of the post-World War II era changed the traditional plant-animal or terrestrial-aquatic dichotomies in ecology. New alignments formed within ecology and new entries into its traditional disciplinary fold have introduced additional points of view to the intellectual framework of ecology [Levin 1976; McIntosh 1974, 1976].

These points of view bear examination in light of the current interest among historians and sociologists of science concerning the hypothesis of the "invisible college" as the basis of the organizational patterns which are associated with major advances and changes in concept (paradigm) in a scientific discipline [Crane 1972; Griffith and Mullins 1972]. This hypothesis is, appropriately enough, based on the logistic curve and suggests that there is a succession in development of a research field—first, rapid growth to a stable (normal) state, and then a decline. Tobey [1977] applied the invisible college hypothesis to the growth of plant ecology in the grasslands in the early 1900s and concluded that the development of grassland ecology, and its major paradigm, succession and climax, is consistent with it (Figure 1).

It is not the author's purpose to explore the invisible college hypothesis in detail, but some of the confusions and contradictions concerning succession and its associated problems may be better understood with a clearer view of the history and sociology of ecology. A common and idealized image of a scientific discipline is that it is universal and that there is free communication and mutual comprehension among its members. In fact it is generally familiar, and the invisible college hypothesis argues that any discipline, particularly one in a state of reorganization, is subdivided into loose networks of scientists with varying degrees of cohesiveness and continuity. In ecological parlance, it is heterogeneous or has pattern and is not in equilibrium. The criteria of such networks, according to Griffith and Mullins [1972] are:

1. Their members believe they are making major changes in concept or methodology. The word revolution is much in evidence.
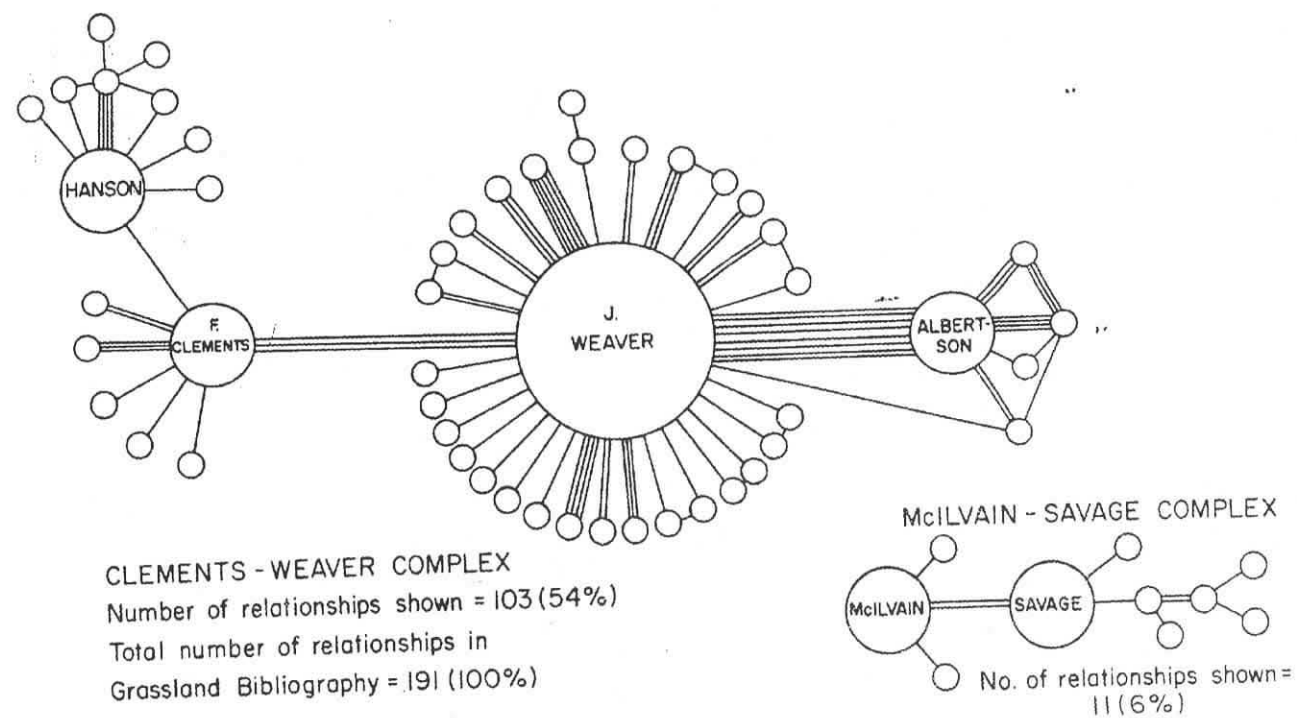
Figure 1. Major Multiple–Authorship Relationships. (Others not shown; spatial configuration for clarity only.) Source: R. Tobey, "American grassland ecology 1895–1955," in *History of American Ecology*, F. N. Egerton, Ed., Arno Press, New York (1977).

Within the figure:

HANSON

F. CLEMENTS

J. WEAVER

ALBERT-SON

CLEMENTS - WEAVER COMPLEX
Number of relationships shown = 103 (54%)
Total number of relationships in
Grassland Bibliography = 191 (100%)

McILVAIN - SAVAGE COMPLEX

McILVAIN    SAVAGE

No. of relationships shown =
11 (6%)

2. They do not consistently observe the attitude of disinterested objectivity desired as a norm for scientists. In fact, they may be passionate and one-sided advocates of a "ruling theory," a danger which T. C. Chamberlain [1890] warned against.
3. There is commonly a close, even somewhat closed, informal communication network within the group. This is manifest in multiple links in a citation network (cf. Figure 1).
4. Typically, a group recognizes one or more outgroups, and the more tightly organized the group is the more it sees itself as opposed to an outgroup.
5. Such groups are commonly, although not restrictively, identified with a leader, who may provide intellectual and/or organizational coherence, although these roles may be played by different individuals. There is usually a place in which the work that the group associates itself with originated, or centers on, and a more or less well defined origin and time span.

Certain developments in recent ecology suggest the existence of invisible colleges and some of the characteristics of these may be seen in the discourse on succession (Table I).

Invisible colleges are held together by identification with a common scientific problem or methodology, and in biology this may be compounded by a common taxon. In some degree they may operate as semiclosed systems and may have a somewhat parochial attitude based on a lack of familiarity with the views of other groups. Not everyone fits neatly into one or the other invisible college by virtue of academic connection or other obvious professional links; but these groups often attract "subway alumni," much as the University of Notre Dame, with which the author is affiliated, does, by virtue of the aura of success that grows about them. The author does not imply that specific assignments are definitive, and it is not necessary for the present purpose that the list be complete. The list is, of course, nationalistic in that

Table I. Tentative Invisible Colleges in Recent Ecology

| Group | Leader | Place | Initial Date |
|---|---|---|---|
| Systems Ecology | Eugene Odum | U. Georgia | ca. 1950 |
| Theoretical, Animal Community Ecology | Robert MacArthur | Princeton U. | ca. 1958 |
| Experimental Animal Population Ecology | Thomas Park | U. Chicago | ca. 1945 |
| Theoretical Evolutionary Ecology | Richard Levins | U. Chicago Harvard U. | ca. 1965 |
| Plant Population Ecology | John Harper | U. C. N. Wales | ca. 1960 |
| Quantitative Vegetation | John Curtis | U. Wisconsin | ca. 1950 |
| Ecological Plant Physiology | Dwight Billings | Duke U. | ca. 1950 |

most of the persons and places cited are Americans. It omits major persons and places in other countries that may be more appropriate focal points for particular developments, e.g., R. Margalef. On a longer time scale, other individuals may clearly be seen as the initiators of some of the major facets of recent ecology, e.g., Charles Elton, G. F. Gause, G. E. Hutchinson, R. Lindeman or H. A. Gleason. The principal point the author wishes to make is the obvious one that there are several divergent positions in current ecology specifically concerned with succession, self-consciously identified with major new developments and bearing suggestive similarity with the invisible colleges of recent studies in the sociology of science. If one doubts their self-awareness, a reading of Fretwell's [1975] eulogy of Robert MacArthur or the preface of Barnard Patten's first volume on systems analysis [1971] will illustrate my point.

The concept of succession, and its corollaries community and stability, are so pervasive in ecology that any of the several invisible colleges one chooses to identify has views on them—implicit or explicit. To understand community or ecosystem stability and succession we must now consider ecological and evolutionary processes as they affect all levels of organization. A major difficulty in dealing with the problems associated with the concept is comprehending divergent approaches which have been introduced into ecology, some of which have their own, sometimes incongruent, conceptualization of the problems. Sometimes the proponents of a new point of view are unfamiliar with earlier ecological work, the thinking of other current groups, or their terminology. They may follow the lead of William Derham, a prominent physico-theologist of the early 18th Century, who purposely avoided reading the works of others so that he could himself write with more originality [Glacken 1967].

Much of the new look in succession is a form of "newspeak" [Orwell 1949], the introduction of new words for terms, ideas and phenomena long familiar to ecologists. One of the earliest words adapted for use in ecology was "pioneer," which became the standard word in the ecological lexicon to describe the early stage or stages of a sere and the life history qualities of the species occupying those stages. Clements [1905] and Gleason [1910] specified great seed production, high seed mobility, high light requirements and ability to tolerate disturbed environments as properties of pioneer species now recognized by proponents of r-selection. The term pioneer and the qualities of what Connell and Slatyer [1977] call "opportunist" species have been part of the intellectual baggage of ecologists for so long that it comes as a surprise to find pioneer placed in quotation marks by these authors, presumably as an unfamiliar term. Pioneer, as a descriptor of a successional stage and of characteristics of species, has been widely ignored in the recent rush to "fugitive," "colonizing" and "opportunistic" species—all without substantial addition to concept or fact of succession.

In keeping with this trend, many recent papers on succession replace the perfectly descriptive, long-used and apt word "disturbance" by "perturbation" (and the bastard nonword perturbate) with similarly little added

insight into succession. Perturbation does not appear in the indices of the major ecological journals up to 1970. It appeared in the famous Brookhaven Symposium [1969] on stability, in Odum's 1971 textbook, in Robert May's [1973] book on stability, in Connell and Slatyer [1977] and is the preferred term in the series on systems analysis edited by Patten [1971]. It is now widely, if variously, used. In some instances it is synonymous with disturbance. In others it distinguishes natural impacts from manmade effects. Perturbations may include clear cutting of forest, fertilizing, fire or removing resident populations of rodents. The last is dignified by the name "perturbation analysis" [Schroder and Rosenzweig 1975]. Perturbation came into ecology in the late 1960s, carrying with it an aura of precision from mathematics and physics, where it has a highly specific meaning. In the physical sciences it is synonymous with small perturbation. It implies a system which differs in minor respects only from a system whose behavior is well understood and completely described—an unusual case in ecology. The substitution of such terms for long-familiar and useful terms in the ecological lexicon derives from the entry of new groups into ecology and also from the tendency of some ecologists to think that the precision, rigor and power of scientific ideas and theories from the so called "hard sciences" are readily imported into ecology along with their terminology.

The title of this chapter shares the same history. Recovery is now commonly applied to changes in community or ecosystem properties following a disturbance [Likens et al. 1978]. Its metaphorical content is powerful, particularly given the current emphasis on managed ecosystems and health of environments. In usage it is a somewhat loaded word for the traditional and well-established secondary succession which has long been defined as the sequence of change following disturbance [Golley 1977]. There is some irony in the fact that Clements, often castigated for his proliferation of ecological terms, is being upstaged by advocates of new terms. One now reads that the process of ecosystem recovery following perturbation proceeds from opportunist to mature stages.

There is, apparently, succession in the sciences—certainly there is a pecking order. Sciences are seen as developing from an immature (pioneer), fact-gathering stage toward, and ultimately to, a mature stage. Craig [1976] wrote:

> The science of ecology has matured dramatically in the last few years. From what was primarily a descriptive science has developed a new, mathematically based, evolutionary ecology.

Rosenzwieg [1976] noted the immaturity of ecology as an inductive (Baconian) science and asserted:

> As sciences mature they develop a hypothetico-deductive philosophy. They progress by generating hypotheses and disproving them in controlled experiments. It is my opinion that such a maturation is now underway in ecology.

The ultimate level of scientific maturity is, of course, the capacity of prediction, and some have seen the development of ecology as a predictive

science [Patten 1971; Levandowski 1972; Kolata 1972; Cody and Diamond 1975] with some cautions expressed [Cook 1974; Johnson 1977]. Harper [1977] wrote, "Plant ecology is becoming a science of vegetation management and for this it has to be a predictive science."

The model is, of course, the hard sciences, notably physics and engineering, and the means is mathematics [Patten 1971]. Various things have been introduced into ecology with the implicit assumption that they might serve as hormone injections from the more mature disciplines to stimulate the maturation of ecology. Among the earliest of these was information theory, and ecosystems [Margalef 1968]. Other recent entries into the rush to clarify changes in entropy. Succession was simply the flow of energy between ecosystems [Margaleff 1968]. Other recent entries into the rush to clarify ecology are linear and nonlinear systems theory, catastrophe theory and spectral analysis. Each of these newer entries into ecology has at least a small invisible college which is added to the established colleges in a disconcerting and unstable mixture. The track record of these in ecology is not established, although any of them can be supported by the universal justification of having heuristic merit. Information theory seems largely to have been unproductive in ecology except for providing an all-purpose measurement in the Shannon-Weaver equation [Johnson 1970]. Linear systems representations persist, although Innis [1975] said, "I do not think anyone argues any longer that biological systems are generally linear." He apparently missed Patten's [1975] statement that natural selection operates "to rid ecosystems of undesirable nonlinear characteristics. . ." The fate of the others in ecology is equally indeterminate at present. Innis [1975] also stated that "mathematics and mathematical sciences are an imposition on and threat to some of the practising biologists. In their own defence they must defame the systems approach insofar as it is identified with maths or computers." Since Innis also commented that "elderly people (past 20) have difficulty learning maths," a great many ecologists are in the defensive class. It is not clear that ecologists have been markedly unreceptive to theoretical or mathematical approaches, as Innis suggests. In fact these have become pervasive in ecology, although some proponents have claimed martyrdom in the process [Fretwell 1975; Van Valen and Pitelka 1974]. It is not beyond the pale for a practicing ecologist to require those introducing external theoretical and/or mathematical constructs into ecology to provide and recognize adequate criteria for the relevance and success of these (or lack of it) and these criteria should be ecological. One does not have to stand in opposition to "hypothetico-deductive" science to note the recurring caveats of Chamberlain [1890], Tansley [1935] and, most recently, A. J. Cain [1975]. Cain wrote: "The golden rule is always to ask questions of the animals, not of the pundits. However vociferously any particular theory in population genetics may be proclaimed, it is still necessary to ask whether it actually applies to any real populations; at present some theories appear to have some of the characteristics of religious dogma" [cf. Tansley 1935].

## A BRIEF HISTORY OF SUCCESSION AND
## COMMUNITY CONCEPTS

A look at modern concerns about succession in the context of the history and sociology of ecology may be instructive. At the very least it may provide for new generations of ecologists an overview of the background of the continued confusion and current controversy; and it may save some reinventing of ecological wheels and redundancy in subsequent discussion and bibliographies. A number of recent frequently cited papers on succession have reviewed aspects of the subject, and some have redemolished the views on succession and climax associated primarily with Frederick E. Clements. Several provide "new" interpretations; none offers substantial new data [McCormick 1968; Drury and Nisbet 1971, 1973; Horn 1971, 1974, 1975ab, 1976; Pickett 1976, Connell and Slatyer 1977]. Golley [1977] provides a collection of reprinted articles and some useful commentary on succession; and Egerton [1977] includes reprints of several classical papers on ecology which bear rereading.

The so-called classical views of succession and the climax and supraorganismic community concepts associated with it are commonly attributed to Clements, and because of his preeminence, to plant ecologists generally. Clements' deductive and universal theories were formalized early in his career, codified in 1916, subjected to extended exegesis, and perpetuated in plant, animal and general ecological textbooks, probably because of their pedagogical convenience, long after many plant ecologists had rejected much of their substance [Egler 1951; Whittaker 1951, 1953]. They antedated, and even contradicted, many of the descriptive and early statistical analyses for which American plant ecology is commonly criticized, and are essentially a product of Clements' philosophical views [Whittaker 1953]. This is not the place to develop the details of Clements' intellectual sources; but it should be clear that his community and succession concepts were lineal descendants of a long tradition of natural philosophy which held that there were design, purpose and unity in nature and that these required a holistic approach to their understanding [Glacken 1967; Egerton 1973; Goodman 1975; Worster 1977; Simberloff in press].

Clements was neither the only nor the last proponent of this tradition in ecology; but his views fed back into philosophy, influenced Jan Christian Smuts in his formalization of the philosophy of holism, and engendered in some ecologists what was described as religious fervor [Tansley 1935]. Clements [1916] described succession as a universal, orderly process of progressive change. He asserted that the community (association *sensu* Clements) developed from diverse pioneer stages to converge on a single, stable, mesophytic community (monoclimax) under the control of the regional climate. He held that the association repeated in its development the sequence of stages of development of an individual organism from birth through death and was orderly and predictable in its development in the same

sense as the development of an individual organism. As succession proceeded, the association came increasingly to control its own environment and, barring disturbance, became self perpetuating or climax. Clements regarded stabilization as essentially a synonym of succession but recognized its limits, writing, "the most stable association is never in complete equilibrium, nor is it free from disturbed areas in which secondary succession is evident." He was the coiner of the phrase "dynamic ecology," and an early proponent of the importance of function and process in succession. Until the arrival of niche theory (ca. 1957), no ground in ecology was more exhaustingly worked over than Clements' association and climax concepts. To his eternal credit he asserted in the first treatise on ecological research published in America [Clements 1905; cf. Goodman 1975] the recently rediscovered maxim that stability in succession is not strictly associated with species diversity, Clements wrote,

> The number of species is small in the initial stages, it attains a maximum in intermediate stages; and again decreases in the ultimate formation, on account of the dominance of a few species.

This, and other insights, are often overlooked in criticisms of Clements' succession theories.

Community concept and succession in America were largely the province of early plant ecologists with the notable exception of Victor Shelford, who asserted the primacy of community in animal ecology and studied successions of fish ponds and of tiger beetles in sand dune succession [Shelford 1911, 1913]. Shelford collaborated with Clements in formulating the biome concept [Clements and Shelford 1939], which, for all its inadequacies, remains the study unit of choice for modern ecosystem ecologists. The importance of synecology was also recognized by the premier British animal ecologist, C. S. Elton [1927], who wrote, "it is clear that the study of the autecology of the numbers of any species involves inevitably a consideration of the synecology of the community in which it lives." Although the concept, or "heresy" [Colinvaux 1973], of the supraorganismic community is commonly attributed largely to Clements, it was in fact, standard doctrine among animal as well as plant ecologists, most of whom shared similar natural history traditions. S. A. Forbes was a primary expositor of the concept of organization in nature, and his article, "The Lake a Microcosm" [1887], is widely cited. His earlier article [1880], "On Some Interactions of Organisms," is a less familiar but explicit statement of the organismic concept, and a prescient comment on population interactions as molding a community and the energetic basis of the ecosystem. Forbes wrote in 1883:

> A group or association of animals and plants is like a single organism in the fact that it brings to bear upon the outer world only the surplus of forces remaining after all conflicts interior to itself have been adjusted. Whatever expenditure of energy is necessary to maintain the existing internal balance amounts to so much power locked up and rendered unavailable for external use. In many groups this latent energy is so considerable and is a liability to

such fluctuation that a knowledge of its amounts and kinds, and of the laws
governing its distribution, is extremely important to one interested in measur-
ing or forseeing the sum and character of the outward tending activities of the
class.

The prominent American animal ecologists, W. C. Allee, A. E. Emerson,
O. Park, T. Park and K. Schmidt [1949], authors of the major mid-20th cen-
tury work on animal ecology, adopted a firmly organismic view of the com-
munity and succession. Allee's own views on cooperation among organisms
were widely published and attributed by Ghiselin [1974] to his Quaker back-
ground. However, since Ghiselin puts Clements in the Chicago school of
ecology and cites "Vernon" Shelford, this may not be precisely correct. In
any event not all the animal ecologists with an organismic concept of com-
munity are Quakers. Alfred Emerson, who was of the Chicago school, was
certainly an explicit proponent of the organismic concept and the evolving
community unit which permeated the thinking of most animal ecologists
[Emerson 1960]. Bodenheimer [1957] reviewed the attitudes of ecologists on
community and stated that the supraorganismic concept was firmly estab-
lished in animal ecology and limnology, but that its empirical bases were not
well established.

Some recent commentators on succession and community attribute a
rather monolithic Clementsian view to plant ecologists and point out its in-
adequacies as a prelude to suggesting new looks for ecologists. It is not
always clear in these presentations that the Clementsian position was, from
its inception, widely criticized and by no means universally accepted among
plant ecologists, although it permeated the textbooks [Egler 1951]. The
Clementsian, supraorganismic, holistic, community and succession concepts
were probably more widely and less critically accepted by animal ecologists
than plant ecologists. Animal ecologists had turned their attention in good
part to physiological or population ecology, left the development of com-
munity and succession concepts to plant ecologists and readily absorbed the
Clementsian positions which fitted their own preconceptions. To many plant
ecologists the community was less well defined and unitary, and succession
less orderly, than Clements suggested. H. A. Gleason and W. S. Cooper were
the most notable American dissenters. Gleason [1917] opposed the rigid
Clementsian views of orderly, progressive succession [McIntosh 1975]. He
asserted, ". . . succession is an extraordinarily mobile phenomenon whose
processes are not to be stated as fixed laws, but only as general principles of
exceedingly broad nature and whose results need not and frequently do not,
ensue in any definitely predictable way." Cooper [1913, 1923, 1926] pro-
duced numerous studies of succession and generally applied the concept of
multiple seres to a climax but was not a doctrinaire follower of Clementsian
concepts. Cooper [1913] wrote the climax forest is "not homogeneous
throughout in character and appearance. It is made up of small patches of
diverse aspect which represent stages in an endless chain of permutations, the
total result of which is that the forest as a whole remains the same, although
a given area is constantly changing." In effect, he described the mosaic view

of climax commonly attributed to more recent ecologists. Sir Arthur Tansley [1920, 1935], the British counterpart of Clements in preeminence, even-handedly rejected Clements' extreme organismic view and Gleason's individualistic concept. He allowed, however, that the community might be compared to a "quasi-organism."

Gleasons' major contribution to ecology was his individualistic concept. This idea, advanced in opposition to the organismic concept of community and succession developed by Clements, although long ignored is now one of the most influential in ecology [McIntosh 1975]. The dichotomy initiated by Gleason is clearly antecedent, if not antebellum, to the anticipated state of ecology at the present time as later comments will show. Bodenheimer [1957] was an unusual dissident from the supraorganismic view among animal ecologists, adopting substantially Gleason's position. According to Bodenheimer:

> Within the biocommunities interactions occur between various species of plants and animals, but even the beginnings of any real integration of the members of the biotic community, the biocoenosis, into a supraorganismic structure have never been demonstrated. As a rule, each species exists within a community in its own right, which is expressed by the different territory of every species as conditioned by its own reaction basis, different from that of all other species. Little active co-operation occurs in the animal community; more often we find a certain mutual tolerance of such species, whose niches overlap partially.

Worster [1977], in a recent book on the origins of ecology, incorrectly sees the organismic tradition extending through W. C. Allee at Chicago but disappearing with his retirement. Pickett [1976] commented that the Clementsian model of succession has been abandoned by modern ecologists but no contemporary model has replaced it. In fact, the succession concept advanced by Margalef [1968] and Odum [1969] continued the substance of the traditional organismic and Clementsian concepts as various ecologists have noted. Odum noted a parallel between succession and the developmental biology of organisms which is redolent of Clements' supraorganism or of Tansley's quasi-organism. He described the ecosystem as a unit of organization undergoing an orderly process of development that is reasonably directional, and therefore predictable, community controlled and culminating in a stabilized (mature) ecosystem. The functional, or ecosystem, approach to succession provided a series of functional criteria (trends to be expected) in lieu of compositional criteria of seral stages. Clements became subject to criticism when he spelled out his successional and organismal community concepts and gave the climax association geographical extent, life form and compositional criteria. Ecosystems ecologists generally avoid this although they continue some of the traditional recognition of climax communities. Patten [1975] followed Emerson [1960] in seeing the ecosystem as an evolutionary entity. Thus, the core of the organismic position espoused by Clements and evident in most traditional animal ecology, although less explicit in specific regional or compositional detail, is still evident in ecosystem ecology.

Ghiselin [1974] said that holism has gradually merged into systems analysis. Cook [1977] notes that Raymond Lindeman's trophic-dynamic aspects of ecology emphasized the relationship of food cycle relationships to succession. According to Cook, Lindeman followed Thienemann, an early proponent of the organismic concept applied to lakes [Bodenheimer 1957]. Cook writes that Lindeman brought energy relations into the analysis of successional development: "It is here that the analogy between the development of the organism to maturity and community changes during the succession finds its fullest expression; and it is the elaboration of this metaphor which has provided continuing inspiration to community ecologists." To exemplify this Cook cites Odum [1977]. Simberloff [in press] states that the organismic concept is "not dead, but rather transmogrified into the belief that holistic study of ecosystems is the proper course for ecology." Simberloff suggests that this is an expression of philosophical tradition continuous with Greek metaphysics and certainly it is continuous with traditional ecology.

Much of the currently evident schism in ecology and the divergent views on succession are continuations and elaborations of the dichotomy which first became dramatically apparent in the contrasting views of Clements and Gleason. The divergence between individualistic and holistic approaches in ecology is manifest in much of the current literature. Connell and Slatyer [1977] comment that Odum's "trends to be expected" in succession derive from the organismic analogy. They write, "This view is based solely on the analogy, not, in our opinion, on evidence." Harper [1977] states,

> "There is an important sense in which our knowledge of terrestrial ecology has been determined by these contrasting philosophies: an individualistic interpretation based on the history of a community and a holistic interpretation that has seen a community dominated by the constraining forces of limited resource or driven towards some stable constrained state."

Eugene Odum [1977] sees what he calls the "new ecology" as dedicated to holism and dealing with the supraindividual levels of organization. Like Clements and others of his predecessors, Odum sees new systems properties emerging in the course of ecological development and a holistic strategy for "ecosystem development," which is his preferred term for succession. Succession theory had, from its earliest Clementsian origins, incorporated the concomitant and reciprocal changes (reactions) on the environment associated with vegetational change. Accumulation of organic matter, increased moisture and nutrient supply, modification of light and general physical environment were part of the traditional concept of succession. In this sense, succession has always been an ecosystem theory and leads directly to the ecosystems approach [Tansley 1935].

Odum [1977], commenting on ecology as a new, integrative discipline, notes the contrary views of reductionists in ecology and succession but does not emphasize that this invisible college also regards itself as the "new ecology." Clements and Odum converge in their descriptions of succession as an orderly, predictable, unidirectional process of change which results in modification of and control over the physical environment and culminates

in a stable (mature) ecosystem. However, it is just the lack of order, direction, uniformity and predictability and the substantial differences in approach to succession that have brought us to yet another symposium. Nothing could be more neatly organized than Clements' deductive, deterministic, organismic system, and Odum's holistic, integrative "new ecology" is its lineal descendant. From Cooper and Gleason on many ecologists have found these views difficult to accept. The problems lie in the observation by Whittaker [1953] which seconds Gleason's observation quoted above:

> "Succession may thus be thought to occur, not as a series of distinct steps, but as a highly variable and irregular change of populations through time, lacking orderliness or uniformity in detail though marked by certain fairly uniform overall tendencies."

A major dichotomy or polarity is still evident in current ecology between advocates of holistic approaches to community or ecosystems and succession and proponents of reductionist, individualistic or population centered approaches [Golley 1977]. Whittaker [1975] noted the lack of a bridge between them. The invisible colleges have shifted, and new foci, personalities and lineages are all too evident. Convergence of precepts may be seen in some cases, but an embarrassing heterogeneity creates great difficulties in assessments of community and succession. What I have described as a polarity, its historical origins and present states, might be better subjected to an ordination, cluster analysis or cladistic analysis if not a Markov process.

## THE "NEW" SUCCESSION OR "RECOVERY FROM PERTURBATION"

Traditional succession studies posed the question, "What is the order of species populations in time?" A 1973 conference on succession addressed the question, "Are there ordered patterns of populations in time?" Some ecosystem ecologists believe that species patterns are largely irrelevant to ecosystem changes over time. The search for regularity and order, which is the traditional hallmark of science, is not as readily pursued in ecology as some would hope. Clearly, progress has occurred since 1903 when H. C. Cowles [1904] described ecology as chaos; however, pattern recognition remains elusive. Robert Whittaker's metaphor, a shimmer of populations, is aptly descriptive, at least for those who believe that populations matter.

Recent critics of succession concepts have commonly concentrated on extreme interpretations of Clementsian succession. Some have emphasized Egler's [1954] distinction between "relay floristics" and "initial floristics" and agreed with his assessment of the latter as a "startlingly new form" in interpretation of old-field succession (Figure 2). Relay floristics (the upper diagram) simply suggests the classical assumption of amelioration of the site by sequential groups of species as unit communities, each presumably making the site unsuitable for themselves but more suitable for invasion by the next group of species. This interpretation was based largely on early studies of
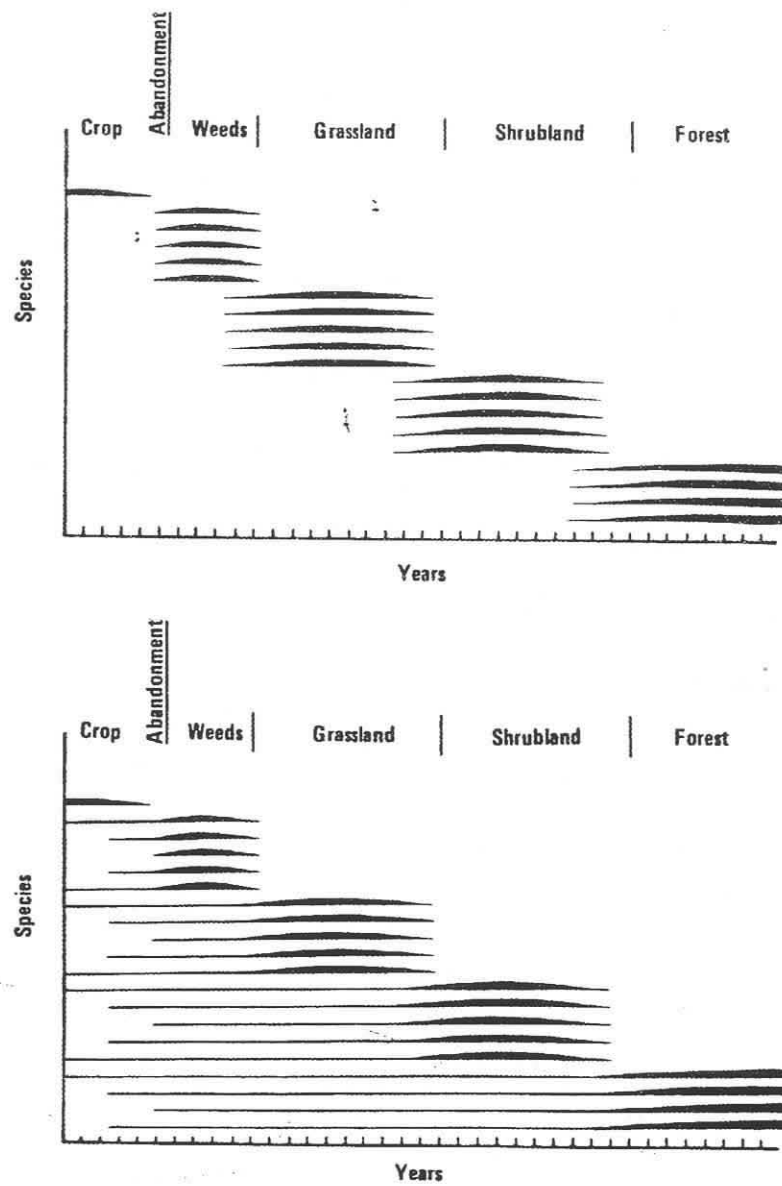
Figure 2. Upper-"relay floristics," lower-"initial floristics." Source: F. E. Egler, "Vegetation science concepts. I. Initial floristics composition, factor in old-field development," *Vegetatio* 4:412–417, Dr. W. Junk bv. Publishers, The Hague (1952–54).

primary succession [e.g., Cowles 1899, 1901] and their incorporation into Clements' organismic successional concept with its emphasis on "reaction" as the effect of organisms in modifying the environment. Relay floristics is a series of unit communities (groups of species) entering and leaving the sere, and rising to peak populations, essentially simultaneously as the members of the successive communities successfully invade the site presumably modified by their predecessors. Vegetation is to Egler, as it was to Clements, "complexes of plant communities existing in nature as organized wholes." Actually, as Egler commented, the general change is one, "of gradual alteration, in which the appearance and disappearance of any one community may be difficult, and needless, to pinpoint." Egler's assertion that the term succession necessarily connotes discrete community jumps is not true. These are assumed only in a restricted theory of succession and of the community unit. Egler's view of a gradual alteration is entirely compatible with other views of succession and is inherent in Gleason's [1917, 1926] individualistic concept and similar concepts current today which are not suggested by Egler's diagrams [McIntosh 1967; Whittaker 1951, 1953, 1967]. Egler, however, regarded succession as a "phenomenon on a high level of sociologic integration, not a matter of individual species." Hence, he preferred the term "development," as does Eugene Odum for similar reasons. Sometimes an interpretation has been placed (not necessarily by Egler) on an individualistic viewpoint which suggests that the plant is independent of effects of other plants or organisms generally, and subject only to the physical environment. That was certainly not Gleason's [1910] view nor that of his successors. Gleason wrote,

> The plant itself is in many cases the controlling agent in the environment....
> The establishment of a plant in the place which it occupies is conditioned
> quite as much by the influence of other plants as by that of the physical
> environment.

His individualistic concept of succession was explicit. "Succession, therefore, as an ecological process, is no more than the mass effect of the action or behavior of individual plants and relates itself perfectly to the individualistic concept of vegetation . . ." [Gleason 1927].

Egler's initial floristic composition was restricted by definition to secondary succession, largely to old fields, and assumed the site to be already populated at abandonment by seeds or vegetative material of the full range of seral stages. These develop without, or with only restricted, invasion of additional species (relay floristics). Species of the initial floristic set assume dominance in sequence, in Egler's diagram, as groups of species rising and falling synchronously. If dissemules of any stage, including the last, are absent at abandonment, that stage cannot readily invade the site and will be absent, or much delayed, waiting on invasion (relay floristics). Egler emphasized the importance of initial floristics in old-field succession, but there is no reason why it should not be generalized to secondary succession at large. The principal point he made is that initial floristics explains certain relatively stable plant communities which change very slowly due to restriction on subsequent invasion of other organisms by the initial populations (Figure 2).

Views and observations on succession have varied greatly among different individuals and invisible colleges, past and present. McCormick [1968], in his admirable general review of succession, noted the views of a number of early plant ecologists on the sometimes surprising persistence of pioneer species in later seral stages and the presence of propagules on disturbed sites. It was no surprise, even to Clements [1916], that a newly bared, secondary succession site might contain viable reproductive units of diverse stages, even the climax, of the sere. He defined primary bare areas as those lacking viable germules of other than pioneer species, having no effect of prior occupation by organisms, and requiring long-term effects of organisms before they are ready for climax communities. Secondary bare areas, he said, "possess viable germules of more than one stage, often in large number, retain more or less of the preceding re- actions, and consequently give rise to relatively short and simple seres." Oosting and Humphries [1940] among others recorded the persistence of viable seed in successional stages of various ages [cf. Livingston and Allessio 1968]. The possibility of residual propagules, abbreviated seres or skipped stages was clearly recognized by plant ecologists even of the old school. That secondary succession following disturbance by cutting of a forest may pro- duce some surprises would not surprise a co-contributor to this book, Dr. Vogel. In his studies of Crex Meadows in Wisconsin [Vogel 1964] he found that when a jack pine forest was clear cut it was immediately replaced by full- blown prairie, although prairie species had not been prominent in the precut forest. They had persisted as suppressed vegetative forms up to 60 years in the forest. Converse observations of forest species developing on grassland, from grubs following cessation of fire, are very much a part of succes- sional observations in the midwest by Gleason and many others [Curtis 1959; Auclair and Cottam 1971].

Essentially, Egler argued that an established vegetation cover resists inva- sion (relay floristics) from the outside—a thesis supported by seeding experi- ments, which have shown that even artificial seeding does not readily replace established vegetation [Sagar and Harper 1960; Juhasz-Nagy 1964, Karpov 1964]. It is not always clear in initial floristics whether the later species to appear are lying dormant through the dominant period of the earlier species or whether they are growing slowly but suppressed and presumably missed in studies of early stages. Egler stressed instances in which a later component of a sere is absent by chance from the initial floristic composition which will then allow persistence of a stable community of an earlier stage. This is a variant of the position of Gleason that the species which will occur on an available site are substantially a matter of probability depending on the availability of seeds and favorable environment. Cooper [1923] provided a diagram (Figure 3) very similar to Egler's initial floristics and noted that even in a primary succession on glacial till, the climax species, spruce and hemlock, may appear in the first year along with the pioneer species [cf. Drury and Nisbet 1973]. Cooper's diagram, unlike Egler's, shows an indi- vidualistic sequence of species rising to dominance and then diminishing. Cooper [1926], however, contrary to Gleason, believed that the community
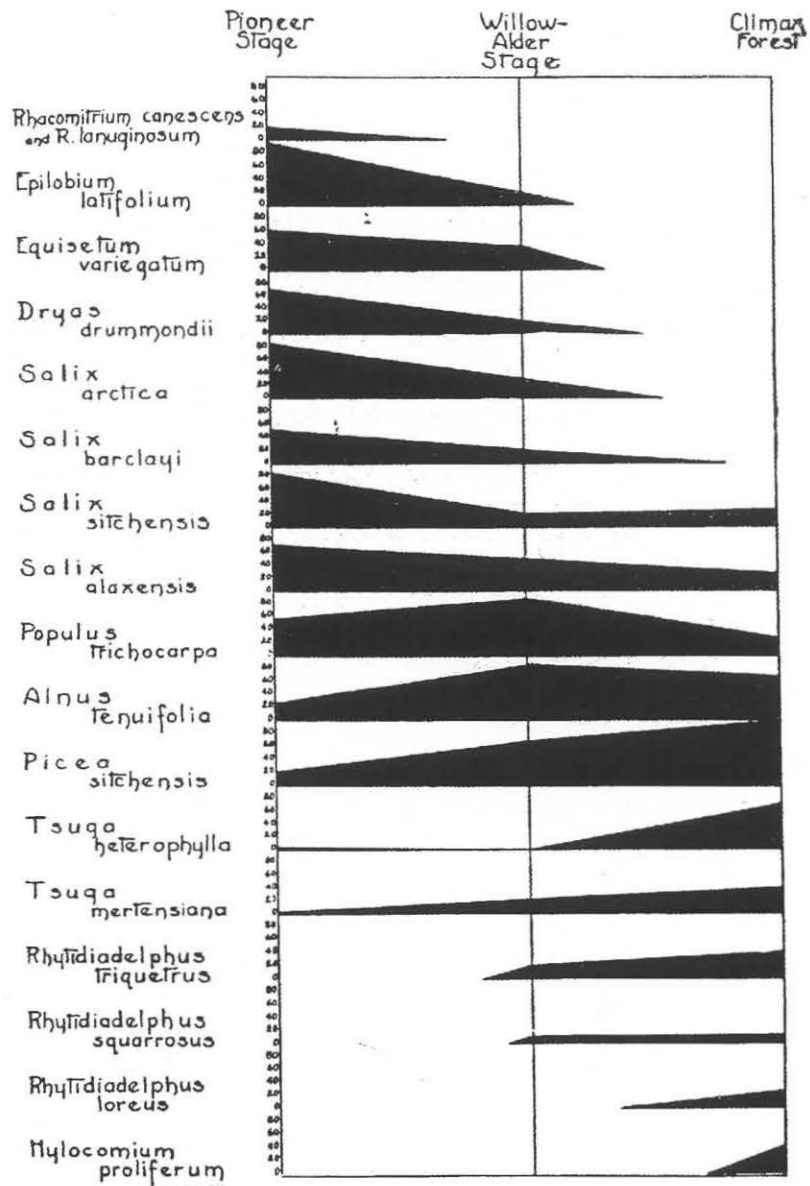
Pioneer
Stage

Willow-
Alder
Stage

Climax
Forest

Rhacomitrium canescens
and R. lanuginosum

Epilobium
latifolium

Equisetum
variegatum

Dryas
drummondii

Salix
arctica

Salix
barclayi

Salix
sitchensis

Salix
alaxensis

Populus
trichocarpa

Alnus
tenuifolia

Picea
sitchensis

Tsuga
heterophylla

Tsuga
mertensiana

Rhytidiadelphus
triquetrus

Rhytidiadelphus
squarrosus

Rhytidiadelphus
loreus

Hylocomium
proliferum

Figure 3. Successional roles of eighteen important species; percentage of total number
of stations in which each was found is shown on the left of the diagram, and indi-
cated by the thickness of the black areas. Source: W. S. Cooper, "The recent eco-
logical history of Glacier Bay, Alaska. II. The present vegetation cycle," *Ecology*
4:223–246 (1923).

was governed by emergent properties, "so that their mass action is not equivalent to the sum of the actions of the component individuals." The fact is that early successional concepts were not all cast in the mold of the Clementsian monolith frequently attacked; there was independent assortment of ideas and conflicting interpretations among plant ecologists. Tansley [1935] raised the question of the meaning of the summation of the actions of the individuals about which Cooper and Gleason differed.

McCormick [1968] noted that classical succession theory is sometimes associated with a theory of geological base leveling, which is vigorously attacked by Drury and Nisbet [1971, 1973]. Although the meaning of Drury and Nisbet's [1971] paper, like Margalef's [1958] paper, is somewhat obscured by the necessity of fitting into the rubric of general systems, they were critical of any successional system which develops in a "preordained course to a stable equilibrium"; they attacked evenhandedly both plant and animal ecologists who urged this. Clementsian plant ecology was criticized for what they described as its analogy with an outmoded theory of geological base leveling and peneplanation–an analogy between peneplain and climax. Drury and Nisbet argued that the assumption that the landscape develops in a pre-ordained course by geological processes to a stable equilibrium predetermines that plant and animal communities will do so. They cited "the classical concepts of cycles of erosion . . . on which the classical theory of plant ecology was based" [Drury and Nisbet 1973]. They advocated replacement of older concepts of geological erosion cycles with a noncyclic kinetic or equilibrium model of geological change. The dispute concerning the geological phenomenon of crustal stability is, according to Wright [1974], "at an impasse" not, as Drury and Nisbet asserted, resolved in favor of the new kinetic model. Whatever the merits of that dispute, it is largely irrelevant to considerations of succession which ecologists generally agree operate on a different time scale from geological base leveling. Clements' theories did not derive specifically from a deterministic view of geomorphology. In all likelihood both concepts derived, as Drury and Nisbet suggested, from a more ancient and powerful tradition of unity, stability and organization in nature extending back to the roots of Greek philosophy [Glacken 1967; Simberloff in press]. In any event, modern plant and animal ecologists do not rest their concepts of succession on geological base leveling or stable climates. Even Clements and Cowles, whose observations on sand dunes influenced Clements' successional concepts, recognized that vegetation cycles were much more rapid than the presumed geological cycles. Cowles early training in geology with Chamberlain no doubt influenced his concept of physiographic succession, but he was explicit in saying that geological factors were not primary [Cowles 1911], contrary to Wright's [1974] interpretations and Drury and Nisbet's assumptions. Cowles wrote:

"It has been seen that changes of climate or of topography generally institute vegetative changes, indeed this would have been predicted to be the case even without examination. But at first thought it seems somewhat striking that far reaching vegetative changes take place without any obvious climatic change

and without any marked activity on the part of the ordinary erosive factors. . . . So rapid is the action of the biotic factors that not only the climate, but even the topography may be regarded as static over large *areas* for a considerable length of time."

Only the most extreme and long since outmoded Clementsian interpretation justified the development of a regional monoclimax on the assumption of geological base leveling [Tansley 1935, Whittaker 1951]. Only Braun among plant ecologists linked vegetation concepts closely to the geological cycle and recent palynological evidence contradicts her interpretation [Wright 1974].

Drury and Nisbet [1971] asserted that the classical Clementsian model excludes reciprocal effects of the plants on the environment and that, "in a rigid extension of the theory, the animals themselves will form a climax community and no interactions between animals and plants need to be considered at all." Whatever the logic of that, plant ecologists were certainly aware of the effects of the plants and animals on the environment. Clements' succession concept was in considerable part based on *reaction* [cf. Drury and Nisbet 1973] which was the effect of plants on the environment. Cowles [1911] commented on the importance to the plant geographer of "the vegetative changes that are due to plant and animal agencies." Clements, Tansley, many of their contemporaries and later plant ecologists recognized that animals could divert the course of succession, control stable communities or even cause retrogression (see below). Has any animal ecologist argued that the existence of stable, efficient animal communities is established, "by assuming that they must have done so in an ancient climax, on an ancient peneplain," as Drury and Nisbet state? Thus, it is not clear why it is necessary to dispute the point.

Drury and Nisbet's [1973] followup article is widely cited and is self described as offering an alternative explanation of succession. They posed their views as alternative to the views of Margalef, MacArthur and Connell (whom they state revived Clements' organismic concept), Odum and Whittaker. They described these authors, collectively, as attributing succession to properties of the community. This article incorporated a basic problem about what succession is and how it is demonstrated. The authors distinguished succession "in space" (zonation) and succession "in time." They commented further, ". . . to provide a unified description on which a general theory can be based, it is necessary to assume a homology between a spatial sequence of zones of vegetation visible at one time on the landscape and a long-term sequence of vegetation types on a single site." This assumption, they asserted is "reinforced by the classical geomorphological theory of landscape development" they claimed in their 1971 paper had led ecologists to view succession as a preordained sequence. For unaccountable reasons, they cite Gleason [1927] by page number as a reference for this assumption. Gleason, like many ecologists, was flatly opposed to such an assumption. He says of the time and space sequences, "never the twain shall meet," and "Areal zonation of vegetation does not constitute a sere, and is correlated with succession

only in exceptional cases." It is not clear who supports the assumption that succession in any current ecological sense refers to other than a sequence in time.

Drury and Nisbet reviewed the applicability of and the evidence for "the Odum-Whittaker criteria" meaning the "trends to be expected" advanced by Odum [1969]. Whittaker's views of succession do not correspond with Odum's sufficiently to hyphenate them; Odum-Margalef would be more acceptable. It is not possible here to examine their review in detail; although it should be noted that they concentrate on secondary, primarily old-field, succession in a temperate forest region. Their summary judgment was that the evidence does not support Odum's "trends to be expected."

Drury and Nisbet offer a "sketch of an alternative explanation" for succession, "based on the observed congruences along environmental gradients" mentioned above. This "observed congruence," is transformed from their assumed homology and has been attacked as a weak link in the successional literature. It is true, as they observe, that only the earliest stages of succession in limited cases, such as old fields, have been directly observed. Many studies, particularly of primary succession, have made the assumption that sites of different age, forming zones in space, may be linked together as a putative chronological sequence [e.g., Cowles 1901; Olson 1958]. Very few have demonstrated a homology between zonation and time. The studies of McCormick and his students of primary succession on granite outcrops, discussed below, are unusual in this respect.

There are numerous difficulties in demonstrating the homology or congruence, as McCormick's studies illustrate. Some critics of succession studies have argued that only a direct observation of change in time, preferably coupled with experiments, can afford adequate evidence [Swan and Gill 1970; Austin 1977]. Hence, the concentration on old-field or microcosm studies. It is familiar that many successions do not occur in time scales convenient for human examination, and it may be nearly impossible to achieve the ideal. An obvious problem in meeting this ideal is the difficulty in finding replicates of long-term time sequences which may be used to demonstrate the presumed common properties of a sere. It is not clear how the "observed congruence" is an "explanation for most of the phenomena of succession . . . as consequences of differential growth, differential survival, (and perhaps also differential colonizing ability) of species adapted to growth at different points on environmental gradients," as stated by Drury and Nisbet.

It is difficult to find in Drury and Nisbet's interpretation of succession something new or "alternative." Their "key statements" are:

1. Rapid dispersal mechanisms and ability to tolerate physical stress of harsh environments are commonly associated.
2. Colonizing ability and growth rate tend to be correlated with size.

These are dubiously listed as "hypotheses" when they are basically empirical observations which, like most ecological observations, are more or less true. It is not clear that rapid dispersal is at a premium if initial floristics is an

important aspect of succession as they intimate. Whatever the validity or novelty of Drury and Nisbet's alternative explanation, they come down firmly opposed to a supraorganismic concept of succession. "A comprehensive theory of succession should be sought at the organismic or cellular level, and not in emergent properties of communities." This may be true, but no clear-cut evidence is advanced by these authors to support the generalization nor is there effective guidance as to how ideas of succession should be integrated with current work in population theory much less with cellular level theory.

Another frequent, if somewhat redundant, contributor to the recent literature and symposia on succession is Horn [1971, 1974, 1975ab, 1976]. Horn [1974] adopted the approach "championed by Drury and Nisbet" [1973] in what he described as "first steps toward theories of succession that are based directly on properties of organisms rather than emergent properties of ecosystems," an approach that Horn characterized as "vitalistic." Horn concentrated on "recent developments in population biology that have profound implications for theories and patterns of secondary succession." He attributed secondary succession to competition; early species "producing an environment in which later species are competitively superior." This places him forthrightly in the camp of the many traditional and some recent ecologists who believe that competition is the major force organizing communities and controlling succession [Diamond 1975; cf. Weins 1977; Pulliam et al. 1977]. It is, therefore, not surprising that in two of his papers Horn commented on Diamond's classification of "supertramps" (pioneer for the birds) which Horn described as, "certainly adaptable to the study of plants in succession." Diamond [1975] developed a widely cited approach which described "assembly rules" for species combinations. The phrase is reminiscent of the early use of "valence" [Raunkaier 1939] which suggested similarly neat combinations for the occurrence of plant species. It would be pleasant to find plant species following a set of combinatorial rules, like elements, on the basis of interspecies competition. However, Connor and Simberloff [in press] have argued that Diamond's assembly rules are either tautological consequences of their definitions or describe patterns which would have resulted from random distribution on islands. What is clear is that concepts of community structure and succession, which are predicted on an assumption of competition as the organizing force, need cautious review; plants may or may not be amenable to Diamond's assembly rules or to Horn's "transition matrix."

Horn [1974] suggested the inadequacies of traditional ecologists stating that much of the conventional wisdom of succession is based on "biased definitions." He provided a definition of what he meant by succession, which turned out to be what ecologists have always meant by secondary succession. If one winnows Horn's several papers on succession, the burden of his new insight into succession is based on perhaps the most maligned aspect of Clementsian successional concept. Horn [1975a] seized on the "dramatic property of succession . . . its repeatable convergence on the same climax

community from any of many different starting points" and noted its
analogy to a statistical process—the Markov chain. From this observation he
moved quickly to the recognition that "Several properties of succession are
direct statistical consequences of plant-by-plant replacement process and have
no uniquely biological basis." The vitalistic interpretation of succession Horn
had seen was replaced by a statistical one leaving "no unique biological basis"
Horn [1975a].

Horn saw a "convergence" of a number of recent workers on the Markov
model which, in his case, rests upon the assumption that the plant-by-plant
replacement probabilities can be determined from the presence of saplings
under adult trees. Horn's [1971, 1974, 1975ab, 1976] data were all gathered
from the same woods behind the Institute for Advanced Study in Princeton
University. He stated [1975a] that forest succession in these woods was
"documented thoroughly" in his publication in American Scientist [Horn
1975b]. Horn's use of the Markov model was based, as he noted, on several
assumptions:

1. Abundance of a sapling under a canopy is a reasonable predictor of survival to
   reach the canopy.
2. These "transition probabilities" do not change with forest composition.
3. The transition probabilities do not change with successional stage or with local
   edaphic conditions.

Horn [1976] commented "If recruitment of young plants is generally pro-
portional to the local abundance of conspecific adults, the consequences for
successional theory are profound." They would be profound indeed, especial-
ly since it was recognized long ago that young tree production most common-
ly is not proportional to conspecific adults and Horn offers no evidence to
the contrary. Horn also observed that saplings can grow in many places
where adult trees cannot. Oddly, he does not comment on the equally pro-
found and familiar observation that adults of many species grow very well in
places where their saplings do not grow. Horn is a recent addition to the long
tradition which recognizes that age structure and reproductive classes give
clues to the future trends of a forest [Daubenmire 1968]. As he commented,
"linear models have made gratifying predictions of what is already known
from earlier crude observations of age and reproduction distributions in
forests." It comes then as no surprise that gray birch or aspen are replaced in
his model by red maple or beech. Horn's promise of "rigorous analysis"
however, still faces the "challenge," [1975a] of a biologically realistic mea-
surement of the transition matrix, which is the essence of his model, based on
demonstration of the validity of the assumption that the presence of a
sapling under an adult tree is a basis for a precise estimate of the probabilities
of replacement of that adult, and that these replacement probabilities do not
change with changes in site conditions or composition. He has made little
apparent progress in meeting this challenge in the several years since he first
enunciated his ideas of succession as a statistical process. Like Levin's alpha
values, the interest of a Markov model lies in the validity of the numbers to

be plugged in and the applicability of the Markov recipe to the biological phenomenon, not solely in its mathematical rigor.

Horn is inordinately fond of distinguishing the trivial from the profound. What may be as trivial as anything he has discovered in the writings of traditional ecologists is that if one could measure the probabilities of each individual adult tree being replaced in situ by one other tree of the same or another species the "patterns of succession are direct consequences of stochastic replacements of one plant by another." Horn's assertion that the process of succession is a statistical result of "direct consequences of ergodic theorems for Markov process" should not be taken as an indication that he entirely neglects biological considerations. He provided [Horn 1971] the mechanism, competition, and in large part the limiting resource, light, which underlies his concept of tree geometry and his theory of forest structure and succession. It is apparent that the biological properties of the plants, especially light tolerance, are an important basis for the transition probabilities. Yet one finds odd juxtapositions in Horn's writings as if his mathematical rigor and logic gets in the way of his biological intuition. Horn [1974] wrote, of succession, "These patterns are independent of biological adaptations to differential successional status, though adaptations affect the speed and clarity of the patterns." The next sentence begins "Appropriate adaptations among early successional species include . . ."

Horn [1974], like Drury and Nisbet, promised "new results" which appear in Horn [1975a]. The crux of anything that may be new is the validity of the assumptions of his model that the presence of a sapling under an adult tree is a basis for estimating the probability of replacing it and that these transition probabilities do not change with change in composition, time or site conditions. These are questionable assumptions [Austin 1977]. Auclair and Cottam [1971], for example, reviewed the dynamics of deciduous oak forest in Wisconsin with particular reference to black cherry. They commented that, "black cherry accounted for approximately one-half of the total numbers in small tree and sapling data. In some cases it was the only tree species in the understory. The shade intolerance of black cherry and lack of evidence that it successfully replaces the oaks directed attention to the probable future of the species." The replacement probabilities of this and other species, in what is probably the best documented forest area in the United States, are much less clear than Horn suggested. They are not proportionate to presence of saplings under adults, but vary on different site conditions, and are influenced by changes in composition [cf. Zedler and Goff 1975]. It is very likely that Horn's probability of the beech replacing itself would change if sugar maple were present in the stands he used to calculate his probabilities of replacement. Forcier [1975] recorded a positive association of beech saplings with sugar maple canopy trees and a negative relation with beech canopy trees. Sugar maple saplings were not significantly associated with canopy individuals of either species. Whittaker and Levins [1977], citing data from Smith, reported that sugar maple saplings were positively associated with beech canopy trees and negatively with sugar maple trees, while beech in this case did not

show much difference. McIntosh [1972], in studies of Catskill Mountain forests, showed that in mixed stands of beech and sugar maple there is a higher ratio of beech saplings to sugar maple saplings than in canopy trees. Size-class distributions suggested that beech and sugar maple are inverse to each other. Beech may replace itself if sugar maple is not present, but not if it is, root sprouts notwithstanding.

The problem is, as Horn [1976] comments in his most recent article on succession, that "The only sweeping generalization that can safely be made about succession is that it shows a bewildering variety of patterns." This is true in his experience even after it has carefully been restricted mostly to secondary succession in a limited forest area. Horn is learning the same lesson that traditional plant ecologists learned previously, namely that succession can be confusing. In 1975 he wrote, "The most dramatic property of succession is its repeatable convergence on the same climax community from any of many different starting points" [Horn 1975b]. In 1976 he wrote, "Succession may lead to alternative stationary states, depending on the initial composition." Horn's [1976] statement, "Analytical models dispel some of the bewilderment by showing that the general pattern of succession is largely determined by biologically interpretable properties of individual species that take part in the succession" may be questioned. He and other ecologists are still bewildered. Horn's question, "Whether succession is convergent or not depends critically on how strongly the amount of recruitment of young plants is determined by the local density of mature plants of the same species?" is an important one. Auclair and Cottam [1971], echoing many earlier ecologists, had already answered it succinctly for a large class of forests. "There is an inverse relation between the importance of trees and saplings of a species." Horn's basic data set is essentially a measure of association of adult trees and saplings, and his transition matrix is based on the probabilities of saplings being associated with canopies of adults. Zedler and Goff [1973] analyzed successional trends in another Wisconsin forest region, using an elaboration of association analysis for size class distributions, and noted an important effect of the size of the sample area on the apparent relations. They said that red maple reproduced abundantly under white and red pine, giving the impression that red maple would replace the pines. In fact, they commented, this almost never happens. Red maple is, of course, a notoriously variable species and may be expected to behave differently in different places. However, the studies of Auclair and Cottam and Zedler and Goff are a substantial step toward the requirement lately seen by Horn [1976]. "The relationship should be explored for a complex community."

Schaffer and Leigh [1976] considered the limitations of mathematical theory in plant ecology and found Horn's assumptions justified. They noted a gross overestimate of red maple in the climax, a peculiarity that Horn's model shares with Leak's [1970] model of forest succession in the northeastern United States. Schaffer and Leigh commented that Horn's model depends on the constancy of the association values which they suggest depend on the "peculiar heterogeneity of the many forest stands that make up

the Institute Woods." The point made by Zedler and Goff that red maple, although abundant under pines, almost never replaced them, suggests the inadequacy of both Horn's Markovian model and Leak's birth and death model both of which predicted large future populations of red maple in mixed hardwood or beech forests.

Pickett [1976] joined Drury, Nisbet and Horn in noting the demise of the Clementsian concept of succession and offered "an evolutionary model of succession which may form the basis of a contemporary model." Like many traditional plant and contemporary animal ecologists, Pickett followed Horn in attributing major importance to competition, past or present, in arranging species in spatial and chronological gradients. He noted the absence of a contemporary model of succession saying that it is "informally approached as a collection of trends, many of which are not parallel or strictly directional." Pickett reviewed the literature which illustrates the effect of "abiotic and competitive selection pressures" in producing individualistic species and subspecific responses to gradients. He then developed the analogy between spatial and temporal (seral) gradients and the analogous causes of species distribution on these gradients. He used "analogy" rather than the more restricted "observed congruence" between spatial and temporal sequences used by Drury and Nisbet [1973].

Pickett developed an evolutionary population-based interpretation of succession specifying the following points:

1. A population cannot be both generalist and a specialist. He commented that selection preserves adaptation to niche and "fosters population coupling" [a phrase that would be grist to Senator Proxmire's mill if it ever appeared in the title of a National Science Foundation award].
2. Succession provides a complex gradient of physical and biotic environments analogous to spatial gradients.
3. Evolutionary strategy [sic] and life cycle characteristics determine the position of a species in a successional gradient.
4. Patches of different successional environments are continuously changing, depending on disturbances, offering different opportunities and selective pressures.

That species have evolved in response to different evolutionary forces in communities is a position with which few ecologists would take exception. Cowles [1904], the American pioneer of the succession, wrote, "If ecology has a place in modern biology, certainly one of its great tasks is to unravel the mysteries of adaptation," and Ganong [1904] provided seven cardinal principles of ecology all concerned with adaptation. A contemporary evolutionary geneticist, Lewontin [1969], saw Clements' theory of succession as "nothing if not an evolutionary theory of the community." Not all that much has been accomplished to link ecology and evolution, but certainly the current effort is now well publicized. Evolutionary strategies, niche and r and k selection are very much in vogue. Harper [1977] commented, "I doubt that we will be able to understand the evolutionary forces operating within plant communities until we have faced the issue of determining the behavior of genets within communities." This admonition to address the intraspecific variation in time and space greatly compounds the difficulties of ecologists

dealing with more than a very limited community. A major, continuing problem lies in determining the effect of selection pressures and population processes in a context of community organization. Classical community and succession theory made it easy as groups of species were assumed to occur together in consistent associations and uniform habitats; thus, the selection pressures were generally such as to "foster population coupling." Alternative concepts of community organization [McIntosh 1967; Whittaker 1967] and divergent views of the forces structuring communities [Weins 1977; Diamond 1978] make the problem of bringing evolutionary, population and community theory together much more difficult.

Pickett's summary point is that "Successional gradients and the evolutionary and functional responses of populations on them are part of a dynamic regional process rather than a single site pattern." It is perfectly reasonable and familiar that different sites may be in different seral stages ranging from pioneer to climax, but to divorce succession from what happens on a single site over time surely is a modification of the entire concept. Any site is manifestly influenced by proximity to seed sources and other organisms that may impinge on it from adjacent sites; it is assuredly part of a landscape pattern. Succession, however, occurs on a site over time and, as noted above, a major failing of succession studies has been seen in their failure to follow the chronological sequence on a single site. Pickett's interpretation of landscape pattern and selection patterns is subject to a number of questions. The relative availability of pioneer sites versus climax sites no doubt varies greatly; in some cases, the incidence of fire for example, fairly accurate estimates may be made of availability of disturbed sites. However, one may doubt his assertion that throughout the history of an area pioneer habitats are numerically common, with diversity limited by environmental severity, and climax habitats less common. Whittaker [1976] remarks on the extreme diversity of the vegetation of areas in the Mideast which are extremely disturbed and severe.

Pickett accepted the assertions of Drury and Nisbet [1971, 1973] concerning the relation of succession of land form and classical succession and developed a three-dimensional representation of a regional vegetational surface (Figure 4) in accord with "modern concepts of geomorphology." His regional vegetation surface showed the response surface of a "succession index" plotted vertically on the plane coordinates of each site. He suggested a number of possible indices with the proviso that the index must be strictly monotonic. Possible candidates were species characteristics, the ratio between system production and respiration, the weighted average of shade adaptation (light tolerance) of species or the average degree of genetic recombination. He saw a coincidence (with slight lags) of biotic and physical parameters. Pickett started his article stating that "the classical interpretation of succession as development of vegetation through discrete stages culminating in a regional climax has been abandoned by modern ecologists." However, his regional vegetational surface was seen as ranging from a low plane surface, or entirely pioneer area, to a high, entirely climax, plane surface with
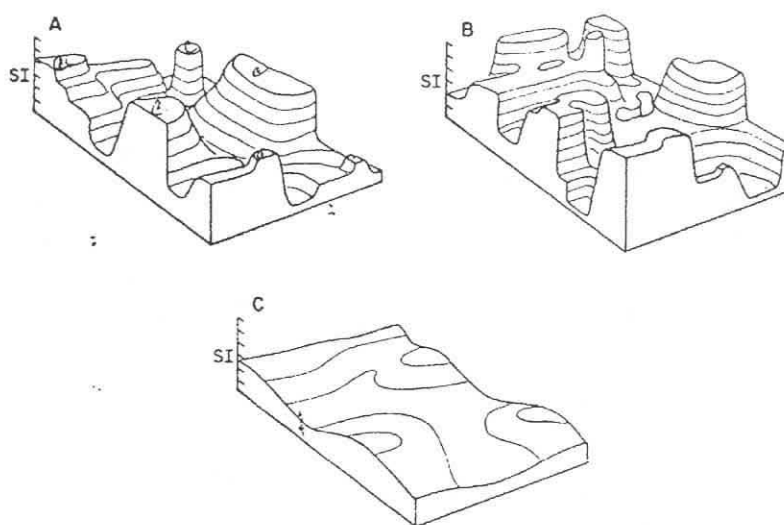
Figure 4. A regional vegetation surface. The x and y plane is a regional map. A mono-
tonic index of successional advancement. SI, is plotted on the z axis. Changes in the
configuration of the surface through time, for example the sequence A–C, illustrates
the successional status and relationships throughout the region. The degree of con-
volution shown by the surface provides an index of $\gamma$-diversity. The region is less
diverse in state C than in A. Species migrate between regions having similar SIs.
Source: S. I. A. Pickett, "Succession and evolutionary interpretation," *American
Naturalist* 110:107–119 (1976).

y diversity = 1, which sounds like a monoclimax. The assumption of a com-
mon montonic index linking all sites with a putative climax does not coincide
easily with "Succession can be understood solely in terms of the interaction
of evolutionary strategies without reference to a deterministic progression
toward climax." The regional vegetational diagram looks very much like a
dissected peneplain.

The most recent evaluation of succession to gain much attention is that of
Connell and Slatyer [1977]. They attempt a codification of models of suc-
cession, review evidence for these, suggest predictions and tests for their
models and discuss stability and community organization. They consider only
the traditional concept of succession as change in species composition, which
some ecosystems ecologists regard as irrelevant [O'Neill 1976]. Connell and
Slatyer, like all their recent predecessors, attack Clements' theory of succes-
sion and climax and indicate that it was so satisfying to ecologists that it has
dominated the field ever since, citing Odum [1969] as its perpetuator. They
note the earlier questions raised by Gleason, but comment that the "queries
and objections have recently increased in number." They do not cite the early
objections of Tansley or the reservations of Cooper; no mention is made of

the most devasting evaluations of Clementsian succession and climax theory of Whittaker [1951, 1953]. In fact, by the time of the "recent increase" in "queries and objections" in the 1960s and 1970s, most of the substance of Clementsian theory (e.g., association, monoclimax, progressive succession and organism) were substantially passé among most plant ecologists; although individuals, e.g., Daubenmire [1968] still carried on substantial elements of Clementsian concepts. Its persistence seems largely to be in textbooks, where its air of universality and orderliness makes for pedagogical convenience. Drury and Nisbet [1973] even found it necessary to attack organismic succession as perpetuated in two high school textbooks. It may also persist because most recent reassessments of succession berate the monolithic stereotype of succession raised by Clements, since it is much more difficult to attack the highly diverse and elusive concepts of succession which are actually held by most ecologists. The major elements of an organismic view of succession are perpetuated in ecosystem ecology in the writings of Margalef and Odum. These authors retain much of the Clementsian concept but shift the emphasis from compositional changes to a regional climax to collective ecosystem attributes such as nutrient or energy flow in the development of unspecified mature ecosystems.

Connell and Slatyer consider the mechanisms of succession noting, first, in contrast to Drury and Nisbet's "observed convergence," the difficulty of reconstructing chronological sequences from spatial sequences. They wrote:

> Second some possible mechanisms have been *ignored*, (italics mine) particularly the effects of grazing animals. The study of succession has in the past been carried out mainly by persons working solely with plants. . . . However, it has meant that the mechanisms concerned have usually been restricted to the interaction of plants with the physical environment or with other plants. The interactions with organisms that consume plants have always been included as one of the many factors influencing succession, but again most of the attention has been given to the consumers involved in the cycling of mineral nutrients, particularly the decomposers such as microorganisms and fungi rather than to animal herbivores.

It is certainly true that succession was mainly developed by plant ecologists, but it is an excessive statement that the effects of herbivores were "ignored." Tansley [1935] wrote that biotic factors such as heavy and continuous grazing, which changes and stabilizes the vegetation, could be a decisive influence. Tansley recognized, for example, the conversion of forest or heath to grassland. Clements coined the word "disclimax" which included, most importantly, deviations from his "true" climatic climax created by the influence of man or animals. Clements recognized extensive areas, rightly or wrongly, as deflected from the "true" pathway of succession, not only by domestic animals but also by prairie dogs and kangaroo rats. He even had a name "therium," fortunately long since discarded, for the latter. Among several early plant ecologists, Sampson [1919] produced extensive studies of grazing effects on western grasslands. In the 1930s and 1940s other range ecologists such as Costello [1944] and Dyksterhuis [1948] studied the effects of grazing on succession. Costello, for example, noted the effects of

kangaroo rats, jack rabbits and harvester ants, the latter in affecting seed supply and providing by their mounds breaks in the vegetation, allowing shortgrasses to enter the succession. Dyksterhius [1948] noted that grazing could arrest a sere and developed the idea of "increaser" and "decreaser" plant species as a measure of the response of vegetation to varying degrees of grazing which was also part of the conventional wisdom of plant ecologists. Other ecologists [e.g., Nelson 1938; Smith 1940; Piemeisel 1945; Ellison 1960; Penfound 1964] recorded effects of both domestic and nondomestic animals on grassland succession.

It might be said that forest ecologists were less emphatic about the role of animals in succession than grassland ecologists, but even here the effect of animals was familiar. Minckler [1946] noted the effect of rodents on tree mortality in old-field succession. Stearns [1946] found that palatable species, such as American yew, largely disappeared from the northern hardwood forest due to deer browsing, and certainly plant ecologists recognized the aptness of Leopold's "plimsoll line" as describing the effect on a forest of intense deer browing. It was long a favorite gambit of plant ecologists to frustrate ecological neophytes by asking them to identify witch hobble (*Viburnum alnifolium*), which looks very different when subjected to deer browse as it frequently was in the 1940s and 1950s. It is heartening to find Connell [1975] stating that much of the experimental evidence for predation as an important factor in community structure is derived from studies of predation on plants by mammals and citing a number of plant ecologists.

The point here is not that plant ecologists knew all about grazing effects or that they had modern quantitative appreciation or studies of the population effects of grazing on plants, but simply to record that they knew a lot more than is implied in the statement that they ignored the effects of grazing. Plant ecologists knew that species were dispersed by grazing and seed eating animals; populations could be sharply reduced or increased under the influence of grazing and browsing; plants differed widely in palatability; and successions could be modified or controlled by native or domestic animals. They were certainly aware of the effects of larger mammalian herbivores, rodents and even a less obvious activity such as mymechory was described in 1906 by Sernander, a plant ecologist. The standard techniques of studying grazing on vegetation, exclosure and enclosure, were described by Clements in his early publications and used by plant ecologists and range managers to illustrate the gross changes in composition of vegetation affected by grazing— short, perhaps, on statistical tests and sophisticated experimental design but hardly ignored.

The irony of the incorrect assumption that plant ecologists ignored grazing is seen in Connell and Slatyer's own procedure:

> We will direct our attention here to the succession of species that occupy the surface and modify the local physical conditions, e.g., plants and sessile aquatic animals. Other organisms such as herbivores, predators, pathogens, 'etc' will be included only when they affect the distribution and abundance of the main occupiers of space.

This is what many traditional plant ecologists did, and for the same reason. It is extremely difficult to encompass all aspects of succession as Connell and Slatyer's exclusions suggest. Except for Shelford, early animal ecologists were generally content to leave succession and the associated concept of community to the plant ecologists. It can be argued, contrary to Connell and Slatyer, that attention of plant ecologists was mostly given to larger animals and all too little to decomposers, such as bacteria, fungi and nutrient cycling, by plant ecologists or anyone else.

The presumed result of ignoring grazing, had that been true, was to focus attention on plant resources and the role of competition in the structure of communities. This did not, as Connell and Slatyer assert, coincide "with the development of a theory of community structure based almost entirely on competition," developed by animal ecologists with a theoretical bent in the late 1950s and 1960s, nor is it newly designated in "recent critical reviews of ecological succession." The belief that competition is a major factor in community organization has, rightly or wrongly, long been explicit in the writings of plant ecologists [Tansley 1917; Clements 1928; McIntosh 1970]. As in many current papers speculating about the role of competition in community structure, actual demonstration of competition was usually lacking, although Tansley and Clements did some of the early experimental studies of competition and Clements wrote the first treatise on the subject. It is quite true that many plant ecologists, like a major "invisible college" of theoretical animal ecologists heavily influenced by MacArthur's work, considered competition a major force in plant communities; but this is a long tradition from the earliest days and extends into recent work of Whittaker [1975]. The illusion that plant ecologists ignored competition is perpetuated by Diamond [1978]. He writes "Even today, plant ecologists tend to stress physical limiting factors almost to the exclusion of interspecific competition," a view which could not be more unrepresentative. Plant ecologists must share with MacArthur and other animal ecologists the credit or onus of asserting the primacy of competition in structuring the community [cf. Weins 1977; Pyke et al. 1977].

One of the difficulties in dealing with the problem of succession is confounding primary and secondary succession. Most of the recent papers analyzing succession have restricted their attention to secondary succession. Connell and Slatyer's paper illustrates this difficulty of dealing with the overall problem of succession in that their commentary and the first step of their proposed series of models restricts their consideration to secondary succession, although they subsequently allude to primary succession and presumably are considering it. They state: "Succession, as represented by steps A through F in figure 1 is the process by which a community recovers from a perturbation." Primary succession involves succession on sites where there is no preexisting community to be perturbed or at least nothing is left of an original community to recover. By definition it is occupation of a site uninfluenced by prior occupancy; it is familiar that prior occupancy has very marked influence on secondary succession.

Connell and Slatyer concentrate their attention on mechanisms of succession which they assert have not been defined clearly or stated as hypotheses subject to field experiment. In a rather inauspicious beginning on definition, they cite Tansley's [1935] paper as equating autogenic succession with absence of abiotic change in the physical environment. Tansley defined autogenic succession as changes induced by the *vegetation*, allogenic succession being anything else. This is the way Egler [1954] uses it, animals being an allogenic factor. Since animal ecologists have taken a hand in succession, autogenic has become synonymous with biotic [cf. Odum 1971]. Connell and Slatyer use autogenic in this sense as the mechanisms which bring about changes in succession. Connell and Slatyer review a number of instances of succession in the context of their proposed model system. It includes a number of interpretations of doubtful validity. For example, although they state that they restrict their considerations to autogenic changes in the absence of significant changes in the physical regime, they cite two examples of changes on a flood plain involving alluvial deposits by floods which are clearly not autogenic as defined by Tansley or as amended by Odum.

Their review of models of succession could be a useful codification of ideas well established in the literature, but the models are not entirely clearly stated nor are the biological examples, to the point in some instances. Connell and Slatyer attribute their model 1 (facilitation model) to relay floristics and models 2 and 3 to initial floristics, which, they state, Egler was the first to distinguish. Egler's reputation as a productive ecologist is safely established on many grounds; it will not diminish it to assert that he provided an apt term for the defining quality of secondary succession, stated by Clements, and laid more stress on it than most earlier ecologists. The point of Egler's initial floristics is that the organisms are not "arriving species." The initial flora is already present at abandonment as either or both seeds and vegetative states. Egler [1954] said, "After abandonment development unfolds from this initial flora, *without additional increments by further invasion* (for the purpose of this discussion)" (italics mine). Connell and Slatyer state that all their models agree on colonizing characteristics of species but differ in the mechanisms that determine subsequent appearance in the sequence. It does not seem likely that models 2 and 3 place the same demand on high seed production, dispersability and ability to tolerate extreme sites as does model 1. Model 1 places a premium on these qualities since the species must seize upon a new site, usually extreme, after it appears; models 2 and 3, if based on initial floristics, produce plants from material already there on a site already modified by organisms. If anything, the premium here is on viability and rapid growth as the seeds could have arrived at their leisure prior to the disturbance which created the opening. They subsequently "predict" that their facilitation model 1 will apply to situations "in which the substrate has not been influenced by organisms before hand." This is by definition a primary succession. This "prediction" has been the basis of interpretation of primary succession from Clements on and experimentally demonstrated by McCormick's work cited below. They follow with comments on secondary

succession predicting that models 2 and 3 will apply there. However, as they note, "If the previous occupation has not influenced the substrate (e.g., on marine rock surfaces), however, model 1 may apply." They have, of course, defined a primary succession, so according to their prediction it should. The statement that the substrate has not been influenced before by organisms must be interpreted carefully. Manifestly, the difference between a primary and a secondary succession is that the latter has a residual effect of prior occupation even if it is laid bare by disturbance. The degree of residual effect and therefore the influence of new occupants on the site is not equivalent in all instances of secondary succession. It is always difficult to fit all organisms into neat categories. In models 2 and 3, for example, Connell and Slatyer state the pioneer species are killed by competition of later plants. Wilson and Rice [1968] and McCormick [1968] report pioneer weeds which commit suicide, presumably by an autotoxic effect, and are unable to replace themselves even in the absence of competitors; allelopathy may have other anomalous affects on succession [Rice 1976].

Connell and Slatyer review the evidence for their models citing some observations of primary successions which support the traditional model of primary succession as mediated by the effects of early species modifying the environment making it less habitable for themselves but more habitable for later arrivals. They find only one terrestrial example of experimental work supporting this view. They ignore the series of studies by McCormick and his students on the development of small terrestrial ecosystems on granite outcrops (Sharitz and McCormick 1973; McCormick et al. 1975; McCormick in press). In this elegant combination of observation and experimental studies of primary xeric succession, they showed the succession of three herbaceous species on bare rock and the influences of increasing soil depth, nutrient supply, water availability, temperature and competition. The zonal sequence in this case is demonstrated to parallel the chronological sequence and is related to the physiological tolerance and competitive abilities of the plants. These pioneer species are restricted on the extreme side of their habitat by abiotic factors and on the more moderate side by competition of other species which perform better in the deeper soils and better nutrient and moisture conditions associated with the expansion of the plant cover over the granite substrate and the weathering of the rock. McCormick commented that the implications of population interactions may be most visible during primary succession and in the pioneer stages.

Connell and Slatyer cite as evidence in intermediate stages the work of Toumey and Kienholz [1931] and Korstian and Coile [1938] as showing that even in the high light levels of early succession forests, the late succession seedlings are suppressed by root competition. They generalize that these experiments indicate that "high tolerance of later successional species to low levels of resources still does not allow them to grow to maturity if they are dominated by a stand of early species." The burden of the trenching experiments was an effort to show the importance of soil moisture as affected by root competition versus light not that later successional species cannot grow

in a stand of earlier species. Studies by Kramer and Decker [1944] showed *why* hardwood seedlings thrived under pine and hardwood stands. Lutz [1945] found that hemlock *had* grown vigorously in the Toumey-Kienholz plots, although pine had died 21 years after the trenching experiments. They concluded that the shade-tolerant hemlock could grow in the pine forest. Oosting and Kramer [1946] reported similar effects in the Korstian-Coile plots; hardwoods were increasing while the pines were declining. The full range of observations in these experiments does not support the conclusions of Connell and Slatyer. In fact, the entire history of ecology in the eastern forest has shown that the early succession pine forests are replaced by later seral species such as hemlock or various hardwoods except on very extreme sites or where disturbance by fire or grazing intervenes. The growth of more tolerant species may be slowed by the presence of earlier species but certainly they do more than simply survive [Curtis 1959; Quarterman and Keever 1962].

Connell and Slatyer's interpretation of succession reminds one that two persons may report of the same water glass that it is half empty or that it is half full. They cite Henry and Swan's [1974] finding that white pines following disturbance dominate the forest for 200–250 years, "suppressing almost all later tree invasion." An old growth white pine forest will commonly have a substantial understory of hardwoods [Curtis 1959], so it is clear that the pines are a one-generation stand. One generation is 250 years; a long time but still only one generation, and successful invasions commonly take place, which is why pine forests did not replace those which were cut. The same generalization may be made of pine forests in the southeast [Quarterman and Keever 1962]. As Connell and Slatyer note, the observation time should be at least as long as the longest generation time of any of the species and any observation period approximating the life span of pines will show that they are being replaced.

Perhaps the major distinctive emphasis of the paper by Connell and Slatyer is that they address the problem of succession in marine aquatic communities; they also emphasize the importance of animals as herbivores (predators) and of pathogens. Although they incorporate all biotic elements they do not endorse the organismic view of the ecosystem and emphasize the population-centered approach to succession.

## HOLISM VS INDIVIDUALISM

The common ground of the several recent reviews and commentaries on successions is:

1. They are explicitly critical of Clements' organismic, holistic concepts of succession and, implicitly or explicitly, of current organismic and holistic views as expressed by Margalef and Odum.
2. They advocate a Gleasonian, individualistic, population-centered approach to succession in contrast to an ecosystem approach.

This may be seen as a simple dichotomy based on a different choice of vantage point from which to view the ecosystem [Levin 1976]. It may, however, be seen as a more fundamental difference in level of maturity within a scientific discipline. Rickleffs [1977] sees ecologists shifting from a Clementsian holistic view of nature toward a Gleasonian or analytical appraisal of nature as a sequence of developmental stages (i.e., maturing). Clearly, not all ecologists have matured in the same direction or at the same rate.

The distinction between the population centered or individualistic position and the ecosystem or organismic position is commonly seen as a dichotomy between reductionist and holistic approaches, although some do not see the sharp distinction [Rosenzweig 1976]. The statements of ecologists may express a tolerant, live-and-let-live attitude [Levin 1976]; but there is generally little doubt where their hearts lie. Lane et al. [1974] wrote in their prospectus that, "a blend of holism and reductionism should be achieved," but in the body of their paper they were less conciliatory:

"In ecology, there has been too much reliance on the assumption that once small portions of the system are studied, the whole can be reconstituted from the parts. There is little theoretical or experimental evidence to support this assumption."

Levins [1968b] was equally explicit:

"Therefore an adequate science on which to base our ecological technology must be holistic, focusing on systems properties of populations and communities."

Odum [1977], like Lane et al. [1974], calls for a combination of holism with reductionism. He comments that a handful of systems ecologists managed to link together some of the reductionists in the Grassland Biome by providing something approaching an ecosystem-level model and thereby almost salvaged the International Biological Program. He sees the "new ecology" as a new integrative discipline that "deals with the supra-individual levels of organization." According to Odum, observations and experiments with natural ecological succession led to a theory that "new ecosystems properties emerge in the course of ecological development and that it is these properties that largely account for the species and growth form changes that occur." He recognizes and says he welcomes the alternative theory based on species-level processes advanced by Drury, Nisbet, Horn, Pickett, Connell and Slatyer. Others are dubious about the merit of that theory. O'Neill [1976] wrote, "There is no a priori reason to believe that the explanation for ecosystem phenomena will be found by examining populations."

Some population ecologists, however, clearly see the role of population-based, evolutionary ecology as providing the basis for understanding of ecosystem phenomena. Foin and Jain [1977], in contrast to Odum [1977], see the lack of a general, ecosystem-level theory as a requirement for "detailed work on populations because the results promise to be more lasting." They view ecosystem description as simply a preliminary to population studies because "understanding of community level processes, at least in

terrestrial plant communities, will largely require solutions to life history tactics in natural communities based on researches on life histories, ecotypic variation, genetic regulation and species interaction." In their view, "holistic approaches and mathematical modeling do not inevitably overcome the traditional barriers to increasing scientific knowledge."

Harper [1977] sees ecology as a triangular science, the vertices being population ecology, production (essentially ecosystem) ecology and community ecology. Harper sees a close parallel between Gleason's individualistic concept of vegetation and the concepts of animal populations, as seen by the animal ecologists, Andrewartha and Birch, which he says are based on historical events. He asserts that the contrasting Clementsian view of community is constrained by its future, an idea which he says has many similarities with the views of the animal ecologists, Nicholson and Varley. The latter, or holistic, interpretation, sees the community as driven towards a stable state and is apparent not only in Clements "climax" but in Margalef's and Odum's "mature" state. Harper wrote, "One of the dangers of the systems approach to community productivity is that it may tempt the investigator to treat the behavior that he discovers as something that can be interpreted as if community function is organized, optimized, maximized or stabilized." He emphatically rejects any holistic idea which suggests that ecosystems are too complex for understanding by reductionists. He urges, as a model, the reductionist approach of biochemists to complex protein molecules where, "the great leaps of understanding were made by those who were willing to simplify the complexity and, as an act of faith assume that the complex whole is no more than the sum of the components and their interactions. The development of plant ecology into a predictive and rigid science depends on a similar willingness . . ." Harper suggests that the important advances in terrestrial plant ecology will come from studies of intraspecific variation within populations and intrahabitat variation. This is a population-centered view with a vengeance.

Antonovics [1976], voicing the position of the "new ecological genetics," said that the individualistic or population-based view of ecosystem is predicated on a typological view of the species. He calls for an escape from such views to thinking of communities as composed of evolving and coevolving species. Antonovics joined Harper [1977] in seeing analysis at the population level as essential to understanding "ecological and evolutionary causation." He regards the "semiphilosophical arguments about the individualistic vs organismal nature of plant communities," and presumably their ecosystem descendants, as "nonoperational." Antonovics urged, as a model, the theoretical studies of animal populations saying that plants are particularly useful for population studies, although he questioned the utility of Lotka-Volterra models.

Schaffer and Leigh [1976] note the much lamented lack of population theory in plant ecology as compared to animal ecology. They review the efforts of a number of ecologists, including Horn [1975], and argue that the theoretical population biology developed by animal ecologists is inapplicable

to plants because of their heterogeneity in distribution, whereas the models of population theory assume homogeneity. Ironically, they ascribe the nonutility of such population theory to the lack of ability to describe. There may be, it appears, some utility in descriptive ecology which has frequently been downgraded [Harper 1977] or pejoratively alluded to as "mere description." Richard Lewontin [1968] voiced the call for an analytic reductionist approach to ecology and frankly deplored "biologists who reject the analytic method and insist that the problems of evolution and ecology are so complex that they cannot be treated except by holistic statements."

The differences between the descendants of the holistic and individualistic conceptualizations of nature continue in current discourse on ecology and succession, and it is useful to recognize the roots of the differences and also the continuity or lack of it [Golley 1977]. Succession to the ecosystem ecologist is a mix of continuance of the traditional concept and break with it. On one hand it continues the organismic tradition of a unitary orderly system with defined properties and predictable trends to a stable state; on the other hand it may ignore the traditional emphasis on change in composition as a major criterion of succession. According to O'Neill [1976] the ecosystem does not change when species change, "Not unless the property or measurement under study changes. It is possible for properties such as nutrient retention time to remain constant even though species change. Further, the identity of the system remains through successional changes in species." This conceptualization of an ecosystem as "fundamentally an energy processing system" whose properties "persist even though populations change" is one pole of the current views of succession. An ecosystem is seen as a definable system with measurable properties which cycles nutrients, transforms energy and produces such collective biological properties as diversity, biomass, productivity, trophic structure and stability as averages of population level processes. Species composition is incidental.

The systems concept of succession as voiced by O'Neill divorces it from compositional change and defines it in terms of change of collective ecosystem properties, e.g., nutrient retention time. In an example of recovery of a deforested northern hardwoods system following clear cutting [Likens et al. 1978], the change in species composition would be incidental to the change in nutrient flows and other ecosystem properties; once these were reestablished it would appear that the ecosystem had recovered independent of its composition. If the identity of the ecosystem remains independent of composition, ecosystem definition must be expressed in measured ecosystem properties. Is the identity seen in any single ecosystem measure or a constellation of measures? How much change in these is allowed within a recognized ecosystem? What if calcium losses are much greater than nitrogen losses and recover more slowly? Are all ecosystem properties equally important? What degree of similarity of any or all ecosystem properties suggest that two ecosystems have converged or that an ecosystem has recovered? How does one map an ecosystem? Foin and Jain [1977] cite as an example of weakening the ecosystem level approach the importance of pin cherry populations

in northeastern forest succession which was seen by Likens et al. [1978] as simply a facet of ecosystem recovery.

An important aspect of much discussion of succession is the coincidence and generality of various ecosystem properties as seen in Margalef [1968] and Odum [1969]. The ecosystem presumably develops from diverse early stages with unlike ecosystem characteristics to a mature stage. Ecosystem properties change from one end of this sequence to the other, usually most rapidly in the early stages. Most of the trends are inadequately documented; the assumed parallel increase of diversity and stability has been the subject of extensive discussion and is now rejected [Goodman 1977]. Vitousek and Reiners [1975] considered ecosystem succession and nutrient retention in forest ecosystems. Contrary to earlier assumptions that as a forest ecosystem matures its ability to conserve nutrients increases, they dissociated vegetational or biotic maturity (climax) from "steady state in the ecosystem sense." According to their interpretation, nutrient losses are higher in both young and mature ecosystems than in intermediate-aged successional ecosystems. From studies on nutrient, especially nitrogen, losses in grassland ecosystems in relation to succession, Woodmansee [1978] asserts that nutrient losses are "not a function of maturing successional vegetational stages." Thus another "trend to be expected" is subject to diverse interpretation.

One of the obvious difficulties in any evaluation of succession is the lack of consistent generalizations which allow any fairly compact overview. Most of the recent commentators on succession have deliberately restricted their scope to secondary, usually old-field, succession in temperate forested areas. This is justified by Drury and Nisbet [1973] on the grounds that there are not adequate observations in nonforested areas to permit generalization. There is in fact a substantial body of succession studies on grasslands, particularly in mixed and shortgrass grasslands [Costello 1944; Ellison 1960; Penfound 1964; Haug 1970]. There are more limited observations in desert and chaparral, and an increasing body of data from arctic and tropical regions [Webb et al. 1972] and aquatic habitats based on both traditional and the "new" ecosystems ecology. The problem is that, contrary to Drury and Nisbet's [1973] assertion that the body of observations is inadequate for generalization, the inclusion of added observations seems to forestall generalization. The restriction in the recent papers on succession of the scope of consideration of a phenomenon, which is often seen as universal, is a retreat from the difficulty of transferring generalizations from secondary successions in temperate forested areas to other areas which don't fit them [Whittaker and Levin 1977]. Generalizations have been, and are still, all too easy to erect on the basis of restricted observation; but as Whittaker and Levin [1977] note, "Time has dealt unkindly with generalizations about succession," from Clements' grandiose monoclimax to the maturity seen by Margalef; the trends seen by Odum are less trendy than anticipated. It remains to be seen whether the ecosystems approach will reveal the organization which makes living relationships symphonic rather than chaotic, as Patten [1976] anticipated, or if the symphony, if found, will resemble one by Beethoven or John Cage.

One of the obvious difficulties in the current discussion of succession is that there are more entrants bringing diverse points of view into a field originally the territory of a limited number of terrestrial plant ecologists. Margalef [1958], a marine ecologist, published his early English language paper in the same journal (Journal of General Systems) in which Drury and Nisbet [1971] published their article on succession. Although both saw their concepts of succession as informed by systems, they came to opposed conclusions about the main aspect of succession. Margalef saw it as a function of an organismic entity, Drury and Nisbet urged a population-centered view. Margalef [1968] saw succession as a process of developing self organization, increasing control of the environment and accumulating energy or information, the more mature communities exploiting the less mature. He asserted that evolution cannot be understood except in the framework of ecosystems and provided a number of characteristics of selection at different successional states. He also provided a list of changes in the ecosystem indicative of its maturity. Slobodkin [1969], in a review of Margalef's book, commented that he indicated the beginnings of several "new and potentially exciting paths" producing a "feeling that sometimes the introspective conviction becomes more poetic than scientific." More to the point, Slobodkin stated that the reader is "forced to do the job that the editors should have done," a statement which could be justly applied to many of the articles and books purporting to supply new insights into ecology in the last decade. Valiela [1971], following Margalef, argued that interchange between communities at various stages is an important aspect of succession. "In a sense the more mature communities would seem to be driving the productive mechanisms of the less mature systems by exploiting the unused energy output." On this basis he questions the meaning of studies dealing with individual stages of succession as separate units.

Much of the discussion in recent reviews and reassessments of succession is confined to terrestrial examples and to limited geographical regions notably temperate forest. Generalizations concerning succession should be widely applicable in both terrestrial and aquatic habitats worldwide. Some of the more confounded discussions concerning succession derive largely from aquatic habitats (e.g., Margalef) or terrestrial areas outside of the temperate forest. Examples which seem compelling in familiar terrestrial forests are less compelling in chaparral, desert or tundra, and even less so in plankton. Succession in aquatic microcosms was compared to forest succession and large bodies of water by Odum [1969]. He saw the same basic trends in microcosms that are characteristic of terrestrial and lake successions. Odum said that succession proceeds in a microcosm in a manner not contrary to classical limnological theory which sees lakes progressing in time from less productive (oligotrophic) to more productive (eutrophic) states. Eutrophication, according to Odum, results from addition of nutrients to a lake from *outside*. In a strict sense this is not succession by his definition, which restricts it to community-controlled processes. In Odum's view, "This is equivalent to adding nutrients to the laboratory microecosystem or fertilizing a field; the system

is pushed back in successional terms to a younger or 'bloom' state." Margalef [1968] also said that oligotrophic lakes are kept at a low level of maturity by nutrients flowing into them. Hutchinson [1969] noted the conventional view of lake succession from oligotrophic to eutrophic and said that a lake could return to the oligotrophic state if the nutrient influx ceases. Eutrophication, like succession, is a concept which apparently lends itself to confusion and controversy. Since eutrophication is commonly associated with increased nutrients and productivity, it is not clear how adding nutrients causes a reversal to a more oligotrophic state when, as Odum comments, a lake will revert to a more oligotrophic state when nutrient input ceases. A complicating factor in aquatic studies is that addition of fish to a fish-free pond may cause a marked increase in standing crop of algae, which is usually taken to characterize the eutrophic state. Hrbáček [1961] showed that introducing fish into a pond depleted the larger zooplankton, which limited the grazing pressure on algae, which increased to a bloom characteristic of a eutrophic state. Chemical analyses showed a similar nutrient content in both oligotrophic and eutrophic ponds. It is difficult to relate these observations to Odum's interpretations of lake succession and to draw parallels with forest succession.

Some aquatic ecologists have disputed the applicability of Gleasons' individualistic concept to aquatic systems on the grounds that it is only applicable to terrestrial organisms. Lane [1978] accused Markarewicz and Likens [1975] of forcing the results of their study of a zooplankton community to fit Gleason's individualistic concept of natural communities. Lane comments, "much of the support for the individualistic concept has come from studies of terrestrial plant communities" and argues that the concept and terminology (importance values, community continuum) associated with it are not relevant to zooplankton communities. Lane states, "there is no particular reason why 1-mm aquatic animals should behave like 10-m trees, nor do carapaces possess the same chemical composition as bark." This is patently in error, as the individualistic concept has been supported by numerous studies of benthic and marine organisms and bird studies, as well as by Makarewicz and Likens. Lane asserts that "macroscopic properties" or "consistent indices" "are characteristic of a type of community" and "vary among different types of communities," and uses Levin's [1968] equations, which measure only "niche overlap" or mutual occurrence, to imply species integration. As Wiens [1977] points out this use is untenable, and it is not clear how Lane recognizes a community type and distinguishes between types. The criterion that the "measures have some intuitive meaning for the investigator" smacks of the traditional intuitive "soziologischer Blick" of some European phytosociologists. However, the major point is that Lane's position rests on the concept of characteristic properties of an integrated community type, and attacks the individualistic concept on the basis of Levins' [1968a,b] holistic properties of communities.

Another set of aquatic observations which is difficult to fit into the concept of orderly succession was provided by Walker [1970]. Walker identified

12 stages in an aquatic succession. He determined from a core the frequencies of transition from one stage to another in a vertical (time) sequence. Far from following a putative sequence of a hydrarch succession, half of the transitions were not in sequence and 17% were regressive.

Discussion of succession is sometimes confused by consideration of scale or lack of it. Connell and Slatyer [1977] state their position on scale and self perpetuation: "So on the scale of generation times and over a large enough tract, if both early and late-successional stages persist despite perturbations both are stable." Pickett [1976] similarly confounded succession as a regional or landscape pattern and a single site pattern. The fact that an early successional stage persists in a landscape is not despite disturbance, as Connell and Slatyer stated, but because of it. The crux of the succession problem is that a species does or does not replace itself on a given site not that it moves successfully to a new site if disturbance makes one available. Succession, climax or stability have enough problems without confusing site stability with landscape or regional stability. Loucks [1970] wrote that succession may be seen as repetitive wave patterns initiated by random disturbances and varying intervals. He examined forest stands on nonextreme sites and suggested that succession and associated community patterns followed wave patterns interrupted by severe disturbances at various intervals. Loucks said that a forest in which changes are taking place should not be regarded as unstable but as part of a series of phenomena making up a stable (homeostatic) system capable of repeating itself whenever a disturbance occurs. Hence, the entire landscape with various stages of the succession may be stable, and various species of the sere which are isolated in the time sequence may be perpetuated. This sounds very much like Clements' original position, which was that the climax association included all of the seral stages. It shifts the stage from the community at any site to a much larger stage, the regional landscape. The whole may in some sense be looked at as a homeostatic mechanism or, as Pickett asserts, a mosaic of successional habitats generated by random or periodic disturbance. That early succession or pioneer areas must recur if certain species are to persist in a region is not in dispute, but this should not be confused with a sequence on a single site. Neither should the existence of a gradational sequence on the landscape be confused with a chronological sequence on a single site. Zedler and Goff [1973] make the point very well. They noted that if their sample area had been as large as a county, the overall mixture of tree composition would have been stable, and at this large scale all species would be "climax" in the sense of persisting in the landscape. As the size of the sample area was reduced the patterns would become more representative of within-stand, or single-site succession, as it is generally understood. It is on this scale that pioneer and climax take on meaning in the ordinary context of succession as abstruse as it may appear. To have both "climax" pioneer and climax species or communities or ecosystems clearly becomes unproductive.

The pattern of vegetation or ecosystems in a landscape has long been visualized as a patchwork of seral stages. In the Clementsian view, these were developing toward, if not reaching, a regional monoclimax with a variety of

semistable communities (subclimaxes), persisting for relatively long periods. Whittaker [1951, 1953, 1974] saw the landscape pattern as a continuous array of both seral and climax communities of several types incorporating the idea that something which was climax on one site could be seral on another. Whittaker and Levin [1977] recognize the landscape pattern as a mosaic of seral and climax stages but emphasize that the pattern on the larger landscape scale is conditioned substantially by types and incidence of disturbance.

The apparent polarities of individualistic and organismic views of succession are complicated by similar polarities which are seen in the factors that control community organization and succession. Traditional plant ecology ascribed to competition a major role in controlling community organization and succession [McIntosh 1970]. A major recent invisible college of theoretical animal ecology, associated with MacArthur, similarly sees competition as the primary force dictating community structure. Cody and Diamond [1975] wrote: "It is natural selection operating through competition that makes the strategic decisions on how sets of species allocate their time and energy; the outcome of the process is the segregation of species along resource utilization axes." Relatively recent opposition to this view is seen in studies suggesting that predation, rather than competition, is the major force structuring communities [Brooks and Dodson 1965; Paine 1969; Wiens 1977; Werner 1974; Pyke et al. 1977]. Pyke et al. state without equivocation: "Thus predation, as determined by the foraging behavior of animals in a community, is the core of community structure.

The ideas of succession and climax were essentially the first theoretical statement of ecology [McIntosh 1976]. Clements framed these in a highly structured, deductive, deterministic theory which provided a central, if much criticized, basis for the development of American plant ecology and which occupied a dominant position in ecological textbooks [Egler 1951]. The search for a universal generalization concerning succession has fared badly as the theory was extended from terrestrial vegetation largely in temperate forest, to other vegetations, to aquatic systems, to animal communities and to the ecosystem. The search was complicated by the change from a relatively simple concept of change of population composition on given sites as the prime criterion to a bewildering array of added criteria accompanied by a new eschatology to replace that of some of the adherents of Clements who demonstrated the fervor noted by Tansley [1935]. The traditional and persistent belief in the unity and balance of nature and the persistence of metaphysical traditions into biological discourse, noted by Simberloff (in press), are contributors to this feeling. According to this tradition, there has to be an organizing principle to the bewildering array of things ecologists see in nature, and if we don't discern it now it is simply because we do not know enough. Some ecologists, in the tradition of Albert Einstein, cannot believe that God plays dice with the ecosystem even though some of the processes are stochastic.

It is perhaps too simple to see the current spectrum of ecologists as two camps searching for significant generalities at the species or ecosystem level

of organization. Yet it is clear that some ecologists see regularities in populations [e.g., Yoda's 3/2 law; Harper and White 1974] and urge that the basis for understanding ecosystems is via an amalgamation of evolutionary genetics and population theory [Lewontin 1969; Harper 1977]. Others look to ecosystem levels for their generalities [Odum 1977].

May [1974] anticipated the "perfect crystals" of ecology; in 1976 he noted there were "many examples where the world appears chaotic and vagarious at the level of individual, species but nonetheless 'constant and predictable' at the level of community organization." "In this spirit" May examined the "intriguing generalization" he attributed to Slobodkin [1962] that the efficiency with which energy is transferred from one trophic level to the next is around 10%. He found that this example of a "constant and predictable value at the level of community organization . . . follows no simple and universal rule" but instead produces "an array of such figures depending on the details of the environments and organisms involved." Nothing daunted, May [1977] returns to the same subject. He notes that many introductory ecology books contain the "grand generalization" that 10% of the energy in any one trophic level is transferred to the next level. [If they do, they should not.] However, as May commented "widely disparate figures" are "a fact which has tended to discourage theoretical activity in this area." This is not the first time, as T. H. Huxley once commented, that a beautiful theory has been killed by an ugly fact. What is not mentioned in May's comments on the 10% efficiency idea is that a symposium [Slobodkin 1970] specifically designed to examine it decided that the empirical evidence did not support it. The author of the idea of the existence of a maximum ecological efficiency thought it fitting that he should be the one to deny it. Slobodkin [1972] commented, "We therefore have no reason to believe that ecological efficiency is in fact constant, and as a matter of fact it is not constant." More generally he said that any theory "containing extensive variables as a necessary component, is to be regarded with suspicion."

There is an anomaly in the fact that the traditional problem of the descriptive plant ecologist, homogeneity, or its converse heterogeneity, is now seen as critical by proponents of opposed points of view. Harper's [1977] recognition of the importance of pattern in Hopkins poetic metaphor "dappled things" is expanded in Whittaker's recognition that the dappling is not static but is, in his metaphor a "shimmer of populations." Schaffer and Leigh [1976] see the pattern inherent in vegetation as limiting the application of mathematical theory derived from animal populations, which Harper sees as a model for ecology.

The problem created by the irregular and changing nature of patterns of ecological phenomena prompted Schaffer and Leigh [1976] to argue that theoretical mathematical population ecology, developed largely by animal ecologists, is not applicable to plants since those theories presume "uniform mixing." It may be questioned on the same ground that these theories are applicable to animals which are not uniformly mixed either. Schaffer and Leigh comment that the relevance of mathematical theory to ecology hinges

ironically on the mathematicians ability to describe, a distinctly old fashioned virtue. The theoreticians task they say is, "to describe spatial heterogeneity in terms simple enough to understand and yet complete enough to predict accurately *how the spatial pattern will develop and change with the passage of time*" (italics added). This problem is what the vertex of descriptive community ecologists of Harper's ecological triangle have wrestled with since the early years of this century with limited success. It remains to be seen if theoreticians will do better if they choose to undertake the task laid on them by Schaffer and Leigh. It is much simpler and mathematically more tractable to assume homogeneity and equilibrium.

The problems of succession are, not surprisingly, integrated with problems of scale and heterogeneity or pattern, both in vegetation and among ecologists. Some of the disputes may be resolved by appropriate consideration of hierarchy and scale and questions of the emergence of properties at higher levels of organization. However, the prospects for rapprochement are not good if reciprocal ignorance persists between the invisible colleges of ecology.

The search for clarity if not unity in succession has daunted ecologists from the beginning. Cowles [1899] posed the difficulty noting that, "the flora of an area must be approached not as a changeless landscape feature, but rather as a panorama, never twice alike. . . . Ecology therefore is a study in dynamics." Cowles [1901] commented: "When we say there is an approach to the mesophytic forest we speak only roughly and approximately. As a matter of fact, we have a variable approaching a variable rather than a constant." Thus, the problem of assessing approach to equilibrium was seen by some early ecologists as they recognized the difficulty of hitting a moving target. The diversity and changing nature of succession was seen by Cooper [1926] in his metaphor of succession as a braided stream. Stanley Cain [1944] expressed the concern that ecology might be too complex for mathematical analysis. Egler said that ecology may not only be more complicated than we think, it may be more complicated than we can think. Golley [1977], perhaps in despair during editing a volume endeavoring to provide an overview of succession wrote, "A simple mechanistic explanation of succession is not possible. Truly there is a rich array of possible mechanisms to explain succession." Whittaker and Levin [1977] consider the problems created by the effects of mosaic phenomena in communities and succession and comment on the bearing of these on the great diversity of ecological theory. They write,

> The failure of unifying statements on succession may not only be historic but predictive. When we discuss communities beyond their most essential attributes as open systems, generality may elude us, except for the generality of diversity. Ecological theory is not precluded by, but should make realistic allowance for, the intrinsic diversity of ecological phenomena; and ecological research must often center on more analysis, interpretation, comparison, and modeling of cases than on widely applicable generalization. Ecologists have sought a theory or master plan of evolution permitting interpretation of communities, through a limited number of strongly linked and widely significant

relationships. Such a theory is naturally desired by ecologists as scientists; but the reasoning of this paper suggests that there may be no master plan except, perhaps, the evolution of such a diversity of relationships as to frustrate that desire.

Such doubts will assuredly not deter those seeking to bring regularity to ecology via information theory, thermodynamics, linear programming, linguistics, systems analysis, catastrophe theory, network theory or transcendental meditation. The contrast in ecology between Levins' noise-free alpha values, Diamond's "assembly rules," Horn's Markovian successions without intervention of biological considerations, Odum's "trends to be expected," May's "perfect crystals" and Whittaker's elusive "shimmer of populations" is evident in much of the discussion about succession today whatever the terminology. The search for satisfying regularity and simplicity is traditional in science, and there is no reason to forgo that search. There is similarly no reason to pursue an illusion that simplicity will be introduced by calling disturbance "perturbation" or secondary succession, "ecosystem recovery" or pioneer "opportunist."

## ACKNOWLEDGMENTS

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